OIKOS 73: 387–398. Copenhagen 1995

Limitation of collared lemming population growth at low densities by predation mortality

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Reid, D. G., Krebs, C. J. and Kenney, A. 1995. Limitation of collared lemming population growth at low densities by predation mortality. – Oikos 73: 387–398.

Populations of the collared lemming (*Dicrostonyx kilangmiutak*) and the tundra vole (*Microtus oeconomus*) have been at consistently low densities, and non-cyclic, at Pearce Point, Northwest Territories, Canada, for six yr. In most summers population densities decline, or only increase marginally, despite ongoing reproduction. We investigated the hypothesis that predation mortality is sufficient and necessary to curtail lemming population growth in summer. To test predictions of the hypothesis, we compared lemming demography, using mark-recapture and radiotelemetry, on a population from which predators were excluded (PE), using a perimeter fence and aerial mesh of nylon (11.4 ha), with demographies of three control populations (18–25 ha). Predation was the proximate cause of the majority of adult and neo-natal mortality, and was not replaced in a compensatory fashion by any other mortality factor in the PE. Significantly fewer adult lemmings died in the PE, and consequently survival inside the PE was significantly enhanced. Recruitment of juvenile lemmings to the adult population was significantly higher in the PE on a per unit area basis. The lemming population in PE followed a significantly different trajectory than the control populations in 1990 and 1991, remaining fairly stable while controls declined. However, the protected population did not grow, apparently because of juvenile dispersal: telemetered juveniles dispersed at an average rate of 53 m/d within the first ten d after weaning. We believe that the protected area was too small to encompass such dispersal, and that emigrants were not replaced by immigrating juveniles since the latter faced heavy mortality outside the exclosure. In 1992, numbers on PE and all controls grew, in conjunction with a regional absence of rough-legged hawks (*Buteo lagopus*) and a scarcity of red foxes (*Vulpes vulpes*), the two principal microtine predators. Tundra vole population growth was also limited by predation mortality, but to a lesser extent. We conclude that predation mortality is sufficient and necessary to limit summer population growth in these microtine species.

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In many regions of arctic North America collared lemmings of the genus *Dicrostonyx* exhibit substantial, and often cyclic, multi-annual population fluctuations. These have been reported for *D. hudsonius* in Ungava (Elton 1942), *D. richardsoni* in northern Manitoba (Shelford 1943, Mallory et al. 1981, Scott 1993), and *D. groenlandicus* near Baker Lake (Krebs 1964), near Igloolik (Rodgers and Lewis 1986), on Devon Island (Fuller et al. 1975), and on the Alaskan north slope (Batzli et al.1980).

Ecological factors causing cyclic population changes have not been experimentally investigated for *Dicrostonyx*, but hypotheses cover the full spectrum of explanations for microtine cycles (Taitt and Krebs 1985, Stenseth and Ims 1993). High densities of *Dicrostonyx*, often in synchrony with brown lemmings (*Lemmus trimucronatus*), are generally followed by strong numerical responses of arctic (*Alopex lagopus*) and red fox (*Vulpes vulpes*) (Elton 1942, Macpherson 1969), ermine (*Mustela*

Accepted 16 January 1995

ISSN 0030-1299

erminea) (Krebs 1964, MacLean et al. 1974) and a number of avian predators (Pitelka et al. 1955, Watson 1957, Maher 1970). Predation by nomadic avian and mammalian predators may synchronize lemming declines over broad geographical regions (Ydenberg 1987, Ims and Steen 1990). Enhanced breeding success by these predators, when lemmings are numerous, increases their numerical response (Watson 1957, Macpherson 1969), and is hypothesized to intensify the depth of the decline in lemming densities and prolong the phase of low density (one or two yr) through strong limitation on population growth (Pitelka et al. 1955, Maher 1967, 1970, MacLean et al. 1974). Similar explanations for the population dynamics of other microtine rodents during the decline and low phase of periodic irruptions have been provided by other studies in North America (Pearson, 1966, 1971, Fitzgerald 1977), and Europe (Hansson 1984, Henttonen 1985, Henttonen et al. 1987, Korpimäki et al. 1991). Limitation by predation mortality is assumed to wane, as predators decline with increasingly scarce prey densities, and eventually be insufficient to limit exponential prey population growth.

The first detailed study of *D. kilangmiutak*, at Pearce Point, on the mainland of the western Northwest Territories, Canada, revealed persistent low densities (less then three per ha) over three consecutive years, and frequent declines in summer populations (Krebs et al. in press). Populations often recovered with winter breeding, as previously observed by Krebs (1964) and Fuller et al. (1975). Predation was the proximate cause of at least 66% of summer mortalities in 1988, and 79% in 1989, leading Krebs et al. (in press) to hypothesize that predation mortality was the most likely factor limiting summer population growth.

This paper reports an experimental investigation of the hypothesis that predation mortality is sufficient and necessary to limit collared lemmings (*D. kilangmiutak*) to low densities at Pearce Point. We tested four predictions of the predation mortality hypothesis: (1) predation is the proximate cause of the great majority of mortalities, (2) predator removal decreases mortality (predation is not replaced by another source of mortality in a compensatory fashion) and therefore increases survival, (3) predator removal enhances rates of population change, (4) predator removal enhances recruitment. We also report demographic data on the tundra vole (*Microtus oeconomus*), the only other common microtine rodent in the area, to look for possible patterns shared with lemmings.

Methods

Study area

The study area (40 km^2) was the vicinity of Pearce Point (69°48'N, 122°40'W), on the south shore of Amundsen Gulf, western mainland Northwest Territories, Canada. The bedrock of dolomites and limestones, interrupted by dikes of basalt, is frequently exposed in cliffed hills rising to 130 m a.s.l. Surficial geology has been influenced by Pleistocene glacial scouring and deposition, and by movement of wind-blown sands in the delta of a local river, draining the Melville Hills to the south.

Population density

Four areas of tundra, each 18 to 25 ha and each including a range of available microtine habitats, were chosen for study grids. Each was fairly discrete, being bordered in part by rocky outcrops or water courses, but partly linked to other areas by continuous similar habitats. Vegetation communities were primarily upland heath (*Dryas integrifolia*/*Carex rupestris*/*Salix arctica*) and mesic tussock (*Carex membranacea*/*Dryas integrifolia*/mosses), and also included some ribbon-like wet meadow (*Carex aquatilis*) bordering water bodies. Collared lemmings occupied drier habitats, and tundra voles occupied the wetter communities on this spectrum (Bergman and Krebs 1993).

On each area we surveyed a grid of reference stakes, and marked all microtine burrows. We quantified the population densities of microtines by live-trapping every one or two weeks from early June (end of snow-melt) to late August (first snow-fall) of 1990, 1991 and 1992, using Longworth live traps, and mark-recapture with ear tags. We used the Jolly-Seber open model for population estimation. In early spring, open traps (ca 60/grid) and nest boxes (ca 12/grid) left over winter were the best places to find microtines, as most burrows were flooded. For an initial trapping session, and alternate ones thereafter, we placed microscope slides covered in talcum powder in all burrow mouths, and examined them 18–24 h later for presence of microtine tracks indicating active burrows (Boonstra et al. 1992). The trapping session then involved immediately setting traps at these active burrows in the morning, and checking them in the afternoon and again in the evening, when they were locked open. At alternate sessions, we used trap locations chosen by tracks on slides the previous session.

To assess how representative our study grids were of regional population patterns, we counted active microtine burrows in 1-ha quadrats located randomly through the study area, both on study grids and elsewhere, in early August 1990.

We rarely caught juveniles more than once. Consequently, we based our density estimates on residents alone, defined as adults plus those few juveniles caught at least twice on the same grid.

For each capture we recorded location, weight and reproductive condition (males – testes scrotal or abdominal; females – vagina perforate or non-perforate, lactating or non-lactating, pubic symphysis closed, partly open or open).

Mortality and litter fates

We fitted adult *Dicrostonyx* with radiotransmitters (Biotrack Inc., model SS-1) mounted to cable ties as neck

Table 1. Characteristics of the predator exclosure (PE) and three control (C1, C2 and C3) study grids.

	PE	C1	C2	C3
Surface cover (%)				
Dryas heath	55.2	65.6	67.1	83.7
Carex-Dryas tussock	39.6	16.1	22.2	9.0
Carex marsh	1.0	0	1.4	0.4
Unvegetated	4.3	18.3	9.3	6.9
Elevation range (m)	8	3	3	25
Distance (m) to				
Natal fox den	4000	3200	2800	1400
Rough-legged hawk nest	200	50	600	2400

collars. Radio and harness weighed approximately 3 g. Individuals were relocated every two or three d on grids, or by extensive searching throughout the study area. This allowed estimation of the date of death to within two or three d. Radios frequently led us to microtine carcasses, remains, or merely the radios in dens or nests of predators. We classified cause of death by autopsy on carcasses, or by assessment of lemming remains and disturbance at burrows.

We used the Jolly-Seber model to estimate survival rates. We also used the Kaplan-Meier procedure for survivorship estimation of radiocollared lemmings, with staggered entry of individuals during the course of the summer, and progressive censoring due to radio failure or survival to the end of the study period (Pollock et al. 1989). To test the possibility that radio packages compromised survival, we followed densities on one of the four grids in 1991 (Control #3) without using any radiocollars.

We assessed the numbers of litters born and their fates indirectly, by monitoring female reproductive condition at least weekly to estimate date of parturition, along with records of her movements and burrow use. Lactating female *Dicrostonyx* typically use one maternal burrow (Brooks 1993; unpubl. data this study), and juveniles are weaned at 15 to 20 d (Brooks and Banks 1973). Termination of lactation, and extensive movements away from a natal burrow before the expected weaning date, were taken as a failure to wean the litter. To assess potential causes of litter mortality, we monitored the natal burrow for evidence of flooding or excavation by predators.

In 1992 we gathered data on juvenile survival and movements immediately after weaning, using miniature radios (weight 1 g; AVM Inc., model SM-1) glued to a small patch of shaved skin on the animal's back. Radio life was 10–14 d, but radios stayed on those lemmings which were not killed only for an average 7.3 d (S.E. 0.83, n = 7).

Predator exclosure

We chose one of the four populations (grids) for a predator exclosure treatment (referred to as PE) to test some of our predictions experimentally. This treatment covered 11.4 ha of an 18-ha grid. Border fence posts were erected in autumn 1989. In June 1990 we constructed a covering, approximately 2 m above ground, to exclude avian predators. This consisted of a lattice of 0.6-cm diameter nylon rope, suspended from iron poles 20 m apart. This lattice supported parallel lines, 0.7 m apart, of monofilament nylon fishing line (14 kg test strength) tightly strung between the lines of rope. In late June 1990 we erected a fence of 2.5-cm mesh chicken wire fencing, around the periphery of the exclosure. This fence stood 1.5 m above ground, with a ground-level apron of 0.3 m either dug into the ground or covered with mud and rocks. The construction successfully lasted three summers and the two intervening winters, with minor repairs.

Mesh size was large enough for microtines to pass through, and they frequently did so. We live-trapped daily for arctic ground squirrels (*Spermophilus parryii*) and ermine, which were taken one to eight km away and released. Sign in spring indicated that fox and ermine entered the exclosure in winter.

Predator populations

We noted raptors prospecting for nest sites in spring, along with their degree of territorial defence. A thorough search of all cliffs within the 40-km^2 area in June gave a complete enumeration of breeding pairs initiating incubation, and their clutch sizes. However, we could not reach nests of glaucous gulls (*Larus hyperboreus*), Thayer's gulls (*Larus thayeri*), and common ravens (*Corvus corax*) on inaccessible cliffs. Breeding success was quantified by visiting nests in early July to enumerate numbers of young chicks, and in mid-August to count young just before or at fledging.

We visited known fox dens biweekly to collect scats, and noted pelage and size of all foxes observed. This allowed us to identify individual foxes based on colour patterns, to count juveniles, and to estimate whether or not young were weaned.

Estimates of ermine activity were based on casual observations, incidental live-trapping and characteristically eaten microtine carcasses, but we did not estimate ermine numbers. In 1991 and 1992 we indexed numbers of arctic ground squirrels by placing microscope slides covered in talcum powder in a fixed sample of burrow mouths and counting the proportion marked within 24 h. Grizzly bear (*Ursus arctos*) activity was based on tracks and casual observations.

Statistics

The predator exclosure treatment was not replicated in any one year. To test for significant deviation of the population parameters in the exclosure from those of the three concurrent control populations, we used the modification of the Student-t test comparing a single observation with the mean of a sample (Sokal and Rohlf 1981: 231).

Table 2. Numbers and breeding success of the principal lemming predators in the study area.

Avian predator	Number of territorial pairs			Number of nests successful (fledglings)		
	1990	1991	1992	1990	1991	1992
Rough-legged hawk	4	6	0	2 (3)	3 (5)	0
Peregrine falcon	5	5	6	5 (10)	2 (2)	4 (10)
Golden eagle	1	1	1	1 (1)	1 (1)	1 (2)
Gyrfalcon	0	0	1	0	0	1 (2)

Mammalian predator	Number of adults			Number of young weaned		
	1990	1991	1992	1990	1991	1992
Red fox	2	3	3 to 1	3	2	0
Ermine	?	?	?	≥1	≥3	≥2
Grizzly bear	1	1	2	0	0	0

Results

Characteristics of study grids

Hummock vegetation was most abundant on PE, and least abundant on C3, but *Dryas* heath showed the reverse pattern (Table 1). The hummock gave more protective cover but had a lower density of *Dryas* food than the heath, so the consequences of this gradient are unclear.

C3 was considerably farther than other grids from a rough-legged hawk nest, but was the closest to the natal fox den (Table 1). C1 probably received more intensive raptor surveillance with its proximity to a rough-legged hawk nest.

Predator community

The predator community varied little between 1990 and 1991, but changed markedly in 1992 when rough-legged hawks did not breed, and red fox breeding failed, followed by disappearance of two of three known adults (Table 2). In spring 1992 we also found the carcasses of three other red foxes which had died during the 1991–92 winter, probably from starvation judging by the poor

Table 3. Fates of resident adult lemmings on control grids (C) with predator access, and in the predator exclosure (PE), during summers of 1990, 1991 and 1992, based on telemetry. Percentages in parentheses.

	1990		1991		1992	
	C	PE*	C	PE	C	PE
Total radioed	67	40	52	25	6	11
Total dying	44 (66)	24 (60)	40 (77)	12 (48)	2 (33)	1 (9)
All predators	39 (58)	23 (58)	38 (73)	11 (44)	2 (33)	0 (0)
All raptors	13 (19)	13 (33)	25 (48)	5 (20)	1 (17)	0 (0)
Rough-legged hawk	7	8	17	4	0	0
Peregrine falcon	0	1	1	0	0	0
Unidentified raptor	6	4	7	1	1	0
All mammals	21 (31)	10 (25)	9 (17)	6 (24)	0 (0)	0 (0)
Red fox	21	8	5	0	0	0
Grizzly bear	0	0	2	4	0	0
Ermine	0	0	0	0	0	0
Ground squirrel	0	2	2	2	0	0
Unknown pred.	5 (7)	0	4 (8)	0	1 (17)	0
Natural death	4 (6)	0	1 (2)	0 (0)	0 (0)	0
Accidental death	1 (2)	1 (3)	1 (2)	1 (4)	0 (0)	1 (9)
Unknown fate	16 (24)	5 (13)	7 (14)	1 (4)	1 (17)	1 (9)
Dispersed	1 (2)	0 (0)	0 (0)	0 (0)	0 (0)	2 (18)
Survived**	6 (9)	11 (28)	5 (10)	12 (48)	3 (50)	7 (64)

*Raptors killed 11 and mammals 5, lemmings before construction completed. Seven (18%) predation deaths occurred inside PE.
**Survived is the number of individuals still alive at the end of the summer.

Table 4. Fates of lemming litters initiated on control areas (C) and predator exclosure (PE) in each summer study period. Percentages in parentheses.

	1990		1991		1992	
	C	PE	C	PE	C	PE
Initiated	35	14	23	38	7	8
Weaned	14 (40)	9 (64)	7 (30)	24 (63)	4 (57)	6 (75)
Lost						
Mother died						
Predation	8 (23)	1 (7)	8 (35)	0	0	0
Unknown cause	1 (3)	0	1 (4)	0	0	0
Storm	1 (3)	0	0	3 (8)	0	0
Infanticide	0	0	1 (4)	2 (5)	0	0
Predation						
Total	5 (14)	1 (7)	4 (17)	5 (13)	1 (14)	2 (25)
Fox	5 (14)	1 (7)	3 (13)	0	0	0
Bear	0	0	1 (4)	4 (11)	0	0
Ground squirrel	0	0	0	1 (3)	1 (14)	0
Ermine	0	0	0	0	0	2 (25)
Unknown fate	6 (17)	3 (21)	2 (9)	4 (11)	2 (29)	0

quality of their bone marrow. We estimated early summer density of arctic ground squirrels at between one and four per km^2. The proportion of slides marked in squirrel burrows in four sample areas within 24 h in late July declined by 55% from 0.38 (S.E. 0.12) in 1991 to 0.17 (S.E. 0.06) in 1992.

Predation mortality – adults

Predation was the dominant proximate cause of death of radiocollared adult lemmings in summer, accounting for between 33 and 73% of mortalities on control grids (Table 3). These are probably underestimates as the fate of 4 to 24% of lemmings and voles remained unknown (Table 3).

Rough-legged hawks and red foxes were the dominant predators in 1990 and 1991 (Table 3). Predation pressure was much reduced in 1992 because rough-legged hawks were absent and foxes scarce. Grizzly bears were occasional visitors in all years, but excavated lemmings on study grids only in 1991. Ground squirrels were persistent but infrequent predators. Ermine were not observed on the study grids except in late 1992, when juvenile ermine killed juvenile lemmings in PE (Table 4). Ermine depredated a mean of 7.6% (S.E. 0.96) of microtine winter nests on the four study grids in winter 1990–91, and 5.3% (S.E. 2.99) in winter 1991–92.

The predator exclosure did not exclude all predation (Table 3). Rough-legged hawks killed lemmings when

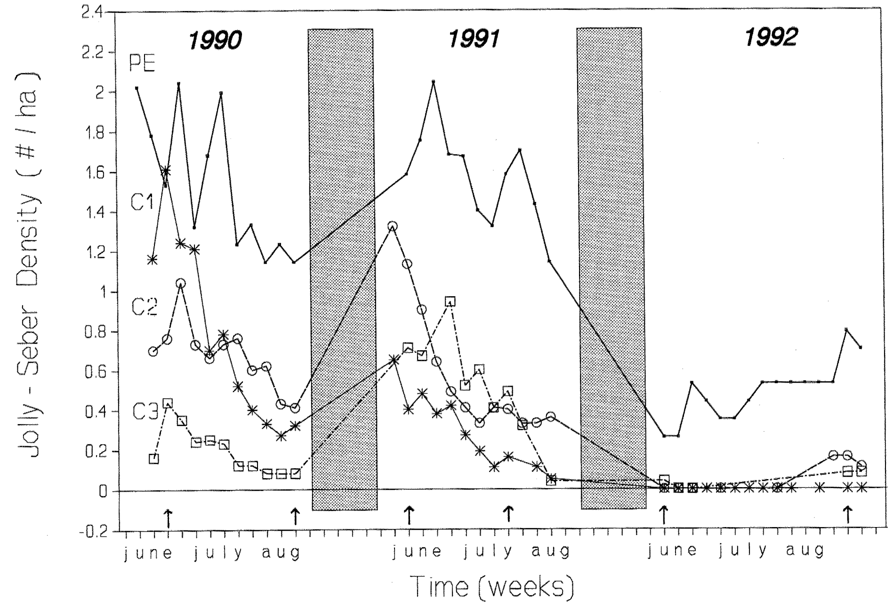

Fig. 1. Jolly-Seber estimates of collared lemming densities in the predator exclosure (PE) and three control grids (C1, C2 and C3) over the three summer study periods. Densities in winter (shaded bars) are interpolated and exact temporal patterns are unknown. Vertical arrows indicate weeks when density comparisons in Table 5 were made.

Table 5. Tests of the null hypothesis that the *Dicrostonyx* density in the predator exclosure was not larger than the mean of sample estimates from control grids (d.f. = 2 in all cases; one-tailed test).

	1990	1991	1992
Beginning* of summer	$t_s = 0.85$ $0.40 < P < 0.50$	$t_s = 1.97$ $0.05 < P < 0.10$	$t_s = 9.15$ $P < 0.02$
End* of summer	$t_s = 4.39$ $P < 0.05$	$t_s = 8.86$ $P < 0.02$	$t_s = 7.68$ $P < 0.02$

*Weeks for which comparisons were made are indicated on Fig. 1.

the nylon was in poor repair or depressed by snow. Ground squirrels dug under the fence, and grizzly bear got in over the fence. Foxes were excluded. In 1990, 16 of 23 (70%) predation deaths inside the exclosure occurred before it had been completely constructed, and the proportion of lemmings lost to predators did not differ between controls (0.58) and PE (0.58) (Chi-square = 0.005, P = 0.943) (Table 3). However, by the end of the summer, the proportion of lemmings still alive was significantly higher in PE (0.28) than on controls (0.09) (Chi-square = 6.446, P = 0.011).

In 1991, the proportion of lemmings killed was significantly lower in PE (0.44) than on controls (0.73) (Chi-square = 6.168, P = 0.013), and a significantly higher proportion were alive at the end of the summer in PE (0.48) than on controls (0.10) (Chi-square = 14.459, P < 0.001) (Table 3).

In 1992, lemming densities were lower than in 1990 and 1991 (Fig. 1), and predator densities declined (Table 2). The proportion of lemmings killed on controls, and in the exclosure, decreased compared to previous years, but sample sizes were too small for statistical tests (Table 3).

Predation mortality – subadults

Predation was the predominant proximate cause of death of lemming litters on all grids; we lack data on fates of vole litters (Table 4). Predators killed litters directly, by entering or excavating burrows, or indirectly, by killing the lactating female. Direct and indirect predation on controls accounted for the loss of 37% of litters in 1990, 52% in 1991 and 14% in 1992.

The proportion of litters lost to predators in PE was substantially less than that on controls in all three years (Table 4). The proportion of litters successfully weaned in PE in 1990 was higher than on controls, but not significantly so (Chi-square = 2.368, P = 0.124). The difference was significant in 1991 (Chi-square = 6.139, P = 0.013). The effect of the exclosure appeared weaker in 1992 with a higher proportion of control litters successfully weaned, but sample sizes were too small for statistical testing.

Other known causes of litter mortality included rain storms flooding burrows, thereby forcing mothers to bring neonates above ground, and infanticide as evidenced by incisor wounds and partial consumption of the body starting with the cranium.

We have few data on fate of lemmings from weaning to sexual adult size. In 1992, when predator densities were relatively low, seven of fifteen weanlings radioed in the exclosure were killed by predators before their radios fell off. Six of the seven, representing three different litters, were killed by ermine at or close to the natal burrows. The seventh was killed by a raptor well outside the exclosure.

Predator exclusion – density

The density of *Dicrostonyx* in PE remained relatively high during summers 1990 and 1991, and diverged from the rapidly declining densities on controls (Fig. 1). The null hypothesis that lemming density in PE was not larger than the mean of control densities holds for estimates at the beginning of summers 1990 and 1991, but can be rejected for estimates at the end of the two summers (Table 5). By late summer PE densities were significantly higher than the mean of control densities (Fig. 2). The

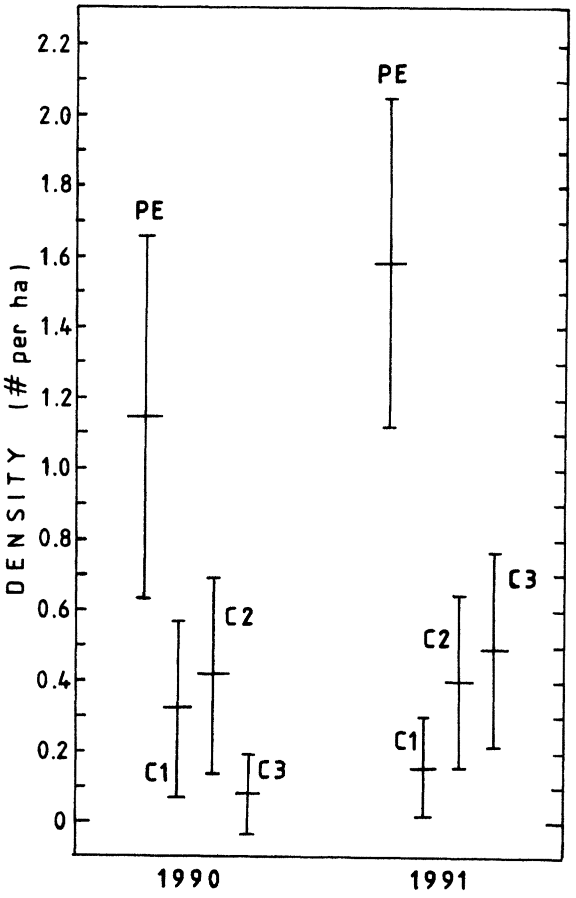

Fig. 2. Jolly-Seber estimates of collared lemming density, and the 95% confidence intervals around these estimates, on the predator exclosure (PE) and three control grids (C1, C2 and C3), in mid-August 1990, and early August 1991.

Table 6. Instantaneous weekly rates of population change (r) for microtine species on the predator exclosure (PE) and three control grids (C1, C2, and C3). N is the period in weeks over which the estimates were made. In blank cells the species was absent or at densities too low for estimation.

	Dicrostonyx			*Microtus*		
	1990	1991	1992	1990	1991	1992
N =	9	10	11	9	10	11
PE	−0.03	−0.03	0.04	–	–	–
C1	−0.18	−0.20	–	−0.12	−0.14	0.13
C2	−0.07	−0.11	0.10	–	–	–
C3	−0.19	−0.29	0.06	0.12	−0.05	0.14

Table 8. Proportion of adult lemmings retrapped after one and after two weeks following initial capture, on C1 and C2 (with radiocollars), and C3 (without radiocollars) in 1991. N is the number of individuals. Test statistic (Chi-square) tests the null hypothesis that C3 does not differ from C1, and C3 does not differ from C2.

Proportion retrapped after	C1 (N = 16)	C2 (N = 29)	C3 (N = 28)
One week	0.56 ($X^2 = 0.084$, $P = 0.77$)	0.52 ($X^2 = 0.468$, $P = 0.49$)	0.61
Two weeks	0.38 ($X^2 = 0.121$, $P = 0.73$)	0.41 ($X^2 = 0.013$, $P = 0.91$)	0.43

instantaneous weekly rate of population change over the summer period was higher in PE compared to the mean of controls in both 1990 and 1991, but not significantly so (1990: $t_s = 1.46$, df = 2, $0.10 < P < 0.20$; 1991: $t_s = 1.69$, df = 2, $0.10 < P < 0.20$) (Table 6).

In 1992 the situation was different. Few lemmings survived the previous winter, and two control grids had no lemmings in spring. The density in PE was significantly higher than the mean of controls both at the beginning and end of the summer (Table 5). In 1992 instantaneous weekly rates of population change were positive in PE and on all controls; populations were able to grow in the relative absence of predators (Table 6, Fig. 1).

The mean density of active microtine burrows on control grids in August 1990 (1.0/ha; n = 6 quadrats) was not significantly different from the mean density on quadrats located randomly through the study area (0.6/ha; n = 11 quadrats) (Mann-Whitney U = 41.5, $P > 0.10$), indicating that control grids adequately represented microtine densities in the study area.

Effect of radiocollars

The Jolly estimates of average probability of survival over four weeks for resident lemmings on C3, without collars in 1991, was higher than survival of radioed residents on other controls in 1990 and 1991, but fell within or close to the 95% confidence intervals for other estimates (Table 7). This difference was not significant in 1991 ($t_s = 2.33$, df = 1, $0.20 < P < 0.40$, one-tailed test). The proportion of adults on C3 (without collars), retrapped one and two weeks after initial capture, was slightly higher than proportions on C1 and C2 (with collars), but differences were not significant (Table 8). The trends in the data indicate that radiocollars slightly compromise lemming survival in the first week after receiving the collar. However, densities on C3 declined in a similar fashion to those on other control grids over the full course of the 1991 summer (Fig. 1, Table 6). We conclude that any negative influence of radio packages on lemming movements and survival is short-lived, and does not significantly affect summer population processes.

Predator exclusion – survival

The Jolly estimator of the average probability of survival over four weeks indicates that resident lemmings survived longer under the predator exclosure than on the three control grids (Table 7). This pattern was significant

Table 7. Jolly-Seber estimates of average probability of survival over a standard four-week period for resident microtines (both sexes combined) on the predator exclosure (PE) and three control grids (C1, C2 and C3). Extreme values of 95% confidence intervals are in brackets. N is the period in weeks over which the data were available. In blank cells the species was absent or at densities too low for estimation.

	Dicrostonyx			*Microtus*	
	1990	1991	1992	1990	1991
N =	8	7	12	8	7
PE	0.62 (0.47–0.76)	0.66 (0.51–0.81)	0.79 (0.5–1.00)	–	–
C1	0.33 (0.19–0.47)	0.25 (0.05–0.46)	–	0.33 (0.09–0.57)	0.45 (0.05–0.96)
C2	0.35 (0.19–0.52)	0.34 (0.17–0.51)	–	–	–
C3	0.25 (0.00–0.50)	0.47 (0.30–0.65)	–	0.63 (0.00–1.00)	0.44 (0.26–0.63)

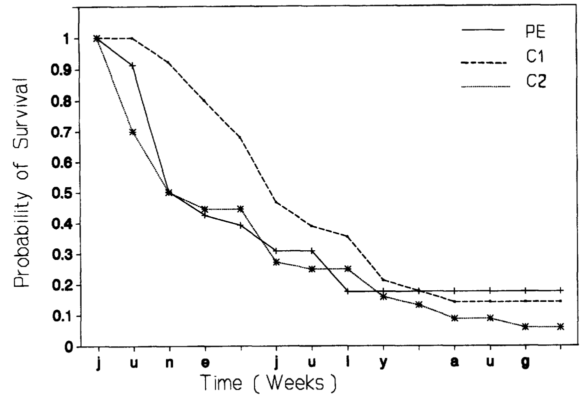

Fig. 3. Kaplan-Meier survivorship functions for collared lemmings in the predator exclosure (PE) and on two control grids (C1 and C2) during summer 1990.

in 1990 ($t_s = 4.803$, df = 2, $P < 0.05$), but not in 1991 ($t_s = 2.118$, df = 2, $0.05 < P < 0.10$).

The Kaplan-Meier estimates showed no significant differences in lemming survivorship curves between PE and C1 (log-rank test statistic = –0.220, P = 0.8), or PE and C2 (log-rank test statistic = –1.499, P = 0.13) in 1990 (Fig. 3). However survivorship in PE stabilized midway through July, when construction was completed, indicating that the exclosure had a strong effect when it operated (Fig. 3).

In 1991 the Kaplan-Meier lemming survivorship curves for PE and C1 differed significantly (log-rank test statistic = –3.432, $P < 0.01$), as did those for PE and C2 (log-rank test statistic = –3.205, $P < 0.01$) (Fig. 4). The exclosure enhanced survivorship of adult resident lemmings, and survival in PE was significantly higher than either C1 ($z = 3.09$, $P < 0.01$), or C2 ($z = 2.83$, $P < 0.01$), by the end of the summer (Fig. 4).

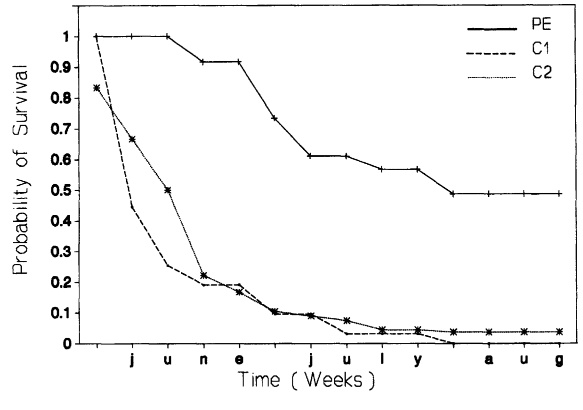

Fig. 4. Kaplan-Meier survivorship functions for collared lemmings in the predator exclosure (PE) and on two control grids (C1 and C2) during summer 1991.

Table 9. The ratio of total adult recruits divided by total first and second litter pregnancies (raw data in parentheses) on the predator exclosure (PE) and two control grids (C1 and C2).

Grid	1990	1991	1992
PE	0.38 (5/13)	0.17 (5/29)	1.00 (5/5)
C1	0.07 (1/15)	0.50 (3/6)	–
C2	0.29 (4/14)	0.33 (4/12)	≥3.00 (3/0)

Predator exclosure – recruitment and population growth

Only juveniles from the first and second summer litters would have grown large enough to recruit as adults during the study periods. Recruits to the adult populations were uncommon on all grids (Table 9), suggesting substantial mortality during dispersal. More juveniles recruited per pregnancy where pregnancies were few (i.e. where densities are particularly low) (Table 9). Perhaps open space encourages settlement, or predation pressure diminishes at very low densities. Even in these circumstances, numbers of recruits per litter were still low, and there must have been substantial mortality, or emigration of juveniles, prior to recruitment.

Recruitment of lemmings to the adult population, after the weaning of the first summer litter, was significantly higher on a unit area basis in PE compared to controls in all years (Table 10). The origin was uncertain for 21 of 25 (84%) recruits on control grids, and 10 of 15 (67%) of recruits to PE. Two recruits to PE were known to come from C1. Only three of 15 (20%) recruits to PE, and four of 25 (16%) recruits to controls, were caught as subadults on the same grid. These data again suggest that juveniles often disperse beyond the population scale chosen for this study. Despite improved recruitment to PE, this protected population did not grow in 1990 or 1991.

Juvenile dispersal

Ten radioed juvenile lemmings were followed for a mean of 5 d after weaning (S.E. 1.13) until their radios fell off (n = 6) or they were killed by a predator (n = 4). All ten left the natal burrow within two d of weaning. Rates of travel were highly variable, and appeared slow in the first

Table 10. Intensity of recruitment (number of recruits per hectare) on predator exclosure (PE) and three control grids (C1, C2 and C3). Sample sizes of recruits in parentheses. Statistics are for the t-test of the null hypothesis that recruitment on PE does not exceed mean recruitment on control grids (one-tailed, d.f. = 2).

Grid	1990	1991	1992
PE	0.44 (5)	0.44 (5)	0.44 (5)
C1	0.05 (1)	0.16 (3)	0
C2	0.22 (4)	0.22 (4)	0.16 (2)
C3	0.08 (2)	0.24 (6)	0.08 (2)
t_s	3.076	4.755	3.896
P	<0.05	<0.05	<0.05

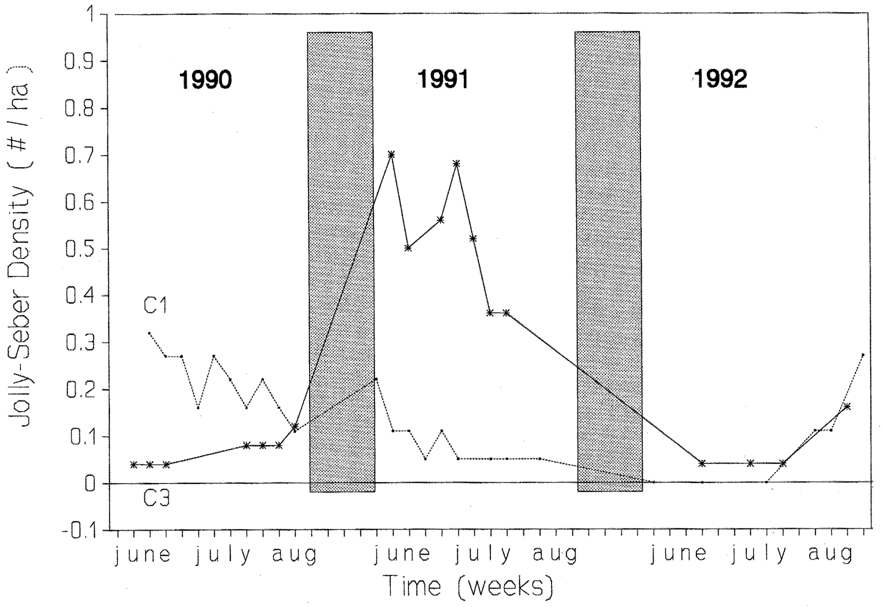

Fig. 5. Jolly-Seber estimates of tundra vole densities on two grids (C1 and C3) over the three summer study periods. Densities in winter (shaded bars) are interpolated, and exact temporal patterns are unknown.

few d after weaning, and sped up for some individuals thereafter. Since they were followed for varying periods, data on distances travelled may be somewhat biased. However, the straight-line distances from natal burrow to last location with a radio gave a mean daily distance travelled of 53.1 (S.E. 17.6, n = 10) m/d. Four of nine weanlings radioed inside the exclosure had left it before their radios fell off, and all four were followed for at least five d.

We gathered daily movement data for four weanlings over periods of five d or more. The mean distances between daily radiolocations for three males were 6, 51, and 126 m, and for one female, 174 m. These juveniles travelled in remarkably straight lines; the sum of daily distances travelled divided by straight-line distance from natal burrow to last location gave values of 1.39, 1.45, 1.38 and 1.20 respectively. The longest daily distance travelled was 600 m.

Tundra voles

Tundra voles existed in appreciable numbers on only two grids (C1 and C3), and were occasional residents on the two other grids (C2 and PE). Vole densities declined on three of four control grids in 1990 and 1991, following a similar pattern to lemmings (Fig. 5). However, they exhibited slower rates of decline than lemmings (Table 6), and the vole population on C3 actually increased in 1990. In 1992, both vole populations increased as did lemmings (Fig. 5, Table 6). The 1992 increase on C1, from zero in spring, resulted from immigration of maturing adults born in the first summer litter. Winter density changes in voles were similar to those in lemmings, with population increases in 1990–91, and declines in 1991–92 (Fig. 5).

We radiocollared adult voles only in 1990. Seven of nine radioed adults were killed by predators (rough-legged hawk, red fox and golden eagle), and two had unknown fates.

The Jolly estimator of vole survival on control grids was slightly higher than that for lemmings on the same grids (Table 7). However, vole survival exceeded the highest observed lemming survival only on C3 in 1990 (Table 7). Average probabilities of survival for resident adult voles without collars in 1991, were intermediate to, and not significantly different ($t_s = 0.22$, $P > 0.50$) than values in 1990 when they wore collars (Table 7).

Discussion

Predation limitation

There are various approaches for investigating whether predation mortality is a sufficient condition to limit prey population growth. Protecting a population by experimentally excluding predators, and comparing the demographic responses of protected prey to control populations, is the most insightful approach (Krebs 1988), and the one we followed. By experimentally reducing the resident predators' access to lemmings, we demonstrated significant reductions in predation mortality, and total mortality, for adult and neonatal lemmings. Also by decreasing predator access, we demonstrated a significant increase in adult lemming survival, and significantly enhanced recruitment of maturing juveniles into the adult population. Consequently, the protected population diverged significantly from control populations in its density trajectory in 1990 and 1991. Overall we confirmed three of four predictions of the hypothesis that predation mortality is sufficient to limit collared lemmings to low densities. The only prediction not satisfied is growth in the protected population.

Our results also indicate that predation mortality is a necessary condition for limitation of collared lemmings at low densities during summer. First, no other mortality factor compensated for the reduction of predation mortality in the protected population. Second, the relative absence of the principal lemming predators, rough-legged hawks and red foxes, in summer 1992 created conditions analogous to a partial regional predator exclusion, and coincided with lemming population growth in all populations, in contrast to negative rates in other years. We do not know, however, at what stage in lemming population growth another limiting factor might operate, making predation mortality unnecessary for curtailing population growth.

The lack of population growth in PE requires explanation. If predation mortality is sufficient to limit lemmings to low densities, experimental removal of such limitation should result in strong population growth. Such growth would be contingent on the following conditions: (1) the experimental setup protects all population processes from predation and thereby adequately mimics regional declines or extinctions of predators; (2) there is no other limiting factor sufficient to curtail growth at low densities; (3) sufficient time has elapsed for theoretically expected time lags (May 1976) to pass.

We doubt that each of these conditions was satisfied. First, the exclosure did not keep out all predators, and was too small to encompass dispersal distances of many weanlings. Consequently potential population growth was curtailed by continued mortality of resident adults, and by predation on weanlings leaving the protected area and on subadults outside the protected area which might have immigrated and recruited to the protected population. We believe that these conditions explain the lack of growth in the exclosure. In summer 1992, with a regional decline in resident predators, two controls and PE showed limited population growth. This resulted from immigration of maturing juveniles born in the first summer litter. These immigrants in turn reproduced. This suggests that a predator removal experiment of sufficiently large scale could lead to population growth.

Second, we only studied summer population processes in detail. In winter limiting factors other than predation mortality might operate. The higher lemming densities in PE compared to controls in spring of 1991 and 1992, indicated that PE was at least partly effective in reducing predation mortality during the preceding winters. However, overwinter rates of population change on all grids were positive in 1990–91 and negative in 1991–92, despite the fact that ermine and red fox bred in both 1990 and 1991, and the proportion of microtine nests depredated by ermine did not differ significantly between these winters. Obviously predation continued in winter but was insufficient to curtail population growth in both winters.

Overwinter population growth results from breeding which occurred in each year of this study, and is common in *Dicrostonyx* (Krebs 1964, Fuller et al. 1975). Perhaps other factors, such as an effect of habitat availability or thermal cover on survival and reproductive success, operate in winter. Whatever the case, winter breeding is necessary for recovery from heavy summer declines, and is likely essential for long-term population persistence as has been indicated by Fuller et al. (1975).

Third, the low density phase is the longest lasting phase in cyclic population fluctuations (Stenseth and Ims 1993). A time lag of approximately nine months in a first-order driving variable generates stable limit cycles of three or four-yr periodicity (May 1976). A likely place for such a time lag to operate is in the low density period. Such a lag has been identified in some Scandinavian microtine species, but without clear evidence of the contributing factor(s) (Hörnfeldt 1994). Under heavy predation risk, theory suggests that individual prey must tradeoff food acquisition with survival (McNamara and Houston 1987). If such behavioural decision-making is not flexible, there may be a time lag as successive generations of prey learn that the world is safer. This may be significant in a predator exclosure experiment for a prey species where risk sensitivity, expressed in depressed rates of growth, maturation or reproduction, has population consequences. For example, with avian predators flying over an exclosure, prey likely still receive stimuli inducing risk avoidance. We have insufficient data to address this possibility. However, our observations of juveniles maturing and breeding during the summer of birth, and litter sizes comparable to those reported elsewhere (unpubl. data; Krebs 1964) suggest that risk sensitivity does not strongly affect potential population growth.

Dispersal

The distances travelled by juveniles within 10 d of weaning are noteworthy as dispersal distances are generally thought to be less than one or two hundred m in microtine rodents (Madison 1985, McShea and Madison 1992). These movements, at low density, traversed many home-range sized areas of unoccupied habitat (unpubl. data). Open habitat is therefore not the only condition necessary for settlement. Perhaps other necessary conditions are the presence of a conspecific of the opposite sex, and the absence of a competitively dominant conspecific of the same sex.

The factors inducing natal dispersal in lemmings are not fully understood. The short time between departure of mothers and departure of weanlings from natal burrows, and the distances weanlings of both sexes travelled, suggest inherent avoidance of local settlement. They have perhaps evolved to avoid inbreeding, or to avoid immediate competition with an adult conspecific of the same sex, especially in males whose adult home ranges and fequencies of movement are substantially greater than those of females at low densities (Brooks 1993). They may also reduce risk of attack by predators (which acquire knowledge of lemming movements and residence by sight and smell) as has been suggested by Brooks (1993) for adult females.

Tundra voles

Similar patterns of population change in voles and lemmings suggest that similar factors limit their populations. Our limited data indicate that predation on tundra voles in summer is severe enough to curtail their population growth. However this limitation is less severe than that on lemmings. Tundra voles are more agile, and live in wetter habitats with more vegetative cover than habitats typically occupied by lemmings. The increase in winter 1990–91 might reflect unmeasured late summer and autumn reproduction in 1990, rather than winter breeding. Vole breeding appeared to last longer in autumn than lemming breeding. We caught no juvenile-sized voles in spring, but the population in spring did include adult-sized females which had not bred.

Reported vole densities were substantially less than lemming densities. This was an artefact of measuring density over all available habitats. Within the wetter vegetation communities used by voles, their densities were similar to or higher than regional lemming densities.

Relevance to population cycles

The preliminary study by Krebs et al. (in press), and data presented here, indicate that lemmings at Pearce Pt. have persisted at densities of less than three per ha for six yr. We conclude that these populations do not exhibit multiannual cyclicity because fluctuations were far less than the order of magnitude shifts in density between peak and low phases reported by Shelford (1943) and Krebs (1964), and generally characteristic of microtine cycles (Taitt and Krebs 1985).

Our data support the hypothesis of Pitelka et al. (1955), Maher (1970) and MacLean et al. (1974), that predation mortality can prolong the period of low density in lemmings. However, lemmings at Pearce Pt. are apparently unable to escape this persistent limitation, which needs explanation.

First, winter breeding may be insufficient to make up for summer declines and ongoing winter losses. Consequently spring densities might never excede levels that migratory, hibernating and resident active predators can limit during the subsequent summer. Autumn densities are so low that winter density increases likely result from multiple litters during the winter. We are currently investigating what factors limit winter breeding.

Second, *Dicrostonyx* habitats at Pearce Pt. are comprised entirely of prostrate species, and lack the the bushy willow (*Salix* spp.) and birch (*Betula* spp.) growth of other regions. This reduced cover increases vulnerability to predation.

Third, the summer predator community at Pearce Point includes many facultative predators (grizzly bear, arctic ground squirrel, golden eagle, peregrine falcon, gyrfalcon, common raven and glaucous gull) which rarely occur together in other tundra regions. Densities of these facultative predators changed little when lemmings were rare in spring 1992. We presume that they broaden their prey base to include such species as arctic ground squirrel, or merely concentrate more on their other foods, such as plants and birds. Only the rough-legged hawk appeared to be an obligate lemming predator, failing to settle and breed in 1992. Red fox and ermine, though generally thought of as microtine specialists, persisted when microtines were scarce, probably by broadening their prey base. Our current investigations of predator diets should help us understand the persistence of such a diverse predator assemblage in this region.

Acknowledgements – We thank the Inuvialuit of Paulatuk, in particular members of the Hunters and Trappers Committee, for permission to do this research on their land. We thank C. Bergman, M. Leung, X. Lambin, B. Scott, N. Williams, J. Ruben, C. Ruben, M. Ruben and J. Ruben for their assistance in the field; and G. White, B. McLean and I. Wingate for planning support. The research would not have been possible without the logistic support of the Science Institute of the N.W.T. (Inuvik Research Lab), the Polar Continental Shelf Project (Canadian Ministry of Energy, Mines and Resources) and the Wildlife Management Division (Renewable Resources Dept.) of the N.W.T. Government. The research was funded by a National Science and Engineering Research Council operating grant to C. Krebs, the Canadian Wildlife Service University Research Support Fund, Northern Scientific Training Grants from the Canadian Dept. of Indian and Northern Affairs, the Arctic Institute of North America Jennifer Robinson Scholarship (1992) to D. Reid, and the Anne Vallee Memorial Scholarship (1991) to D. Reid.

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