Limitations to collared lemming population growth in winter

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Abstract: We investigated the roles of ermine predation and temperature and snowfall regimes in limiting population growth of collared lemmings (*Dicrostonyx kilangmiutak*) at low densities (<3/ha) in winters between 1987 and 1992 at Pearce Point, Northwest Territories, Canada. We estimated winter population growth, for four study populations, as the instantaneous weekly rate of population change from late August to early in the subsequent June. Population growth was not significantly related to the intensity of ermine predation, based on data from two winters. Variance in rates of growth among five winters was significantly explained by a combination of (*i*) cold intensity in autumn, i.e., the mean daily temperature in September and October, when lemmings change from summer to winter morphology, and (*ii*) the insulative potential of the snow, i.e., centimetre-days of snow cover per degree-day of frost from November through March, when lemmings potentially breed. Arvicoline winter nests were strongly associated with remnant snow in spring, indicating selection for areas with deepest snow. Low autumn temperatures and shallow winter snow appear to be strong limiting factors in winter, and may prolong the period of low density of *Dicrostonyx* populations.

Résumé : Nous avons étudié l'influence de la prédation par les hermines, de la température et du régime nivéen sur la croissance des populations de Lemmings variables (*Dicrostyonyx kilangmiutak*) de faible densité (<3/ha) en hiver de 1987 à 1992 à Pearce Point, dans les Territoires du Nord-Ouest, Canada. Nous avons estimé la croissance de quatre populations en hiver en utilisant comme indice de croissance le taux hebdomadaire instantané de changement dans la population entre la fin d'août et le début du mois de juin de l'année suivante. D'après les données accumulées au cours de deux hivers, la croissance démographique n'était pas en corrélation significative avec l'importance de la prédation par l'hermine. La variance dans les taux de croissance, d'hiver en hiver au cours de 5 années, est reliée significativement à la combinaison de deux facteurs (*i*) l'intensité du froid à l'automne, i.e., la température quotidienne moyenne en septembre et en octobre, au moment où les lemmings acquièrent leur morphologie d'hiver et (*ii*) le potentiel isolant de la neige, i.e., centimetre-jours de couverture de neige par degré-jour de gel entre novembre et mars, lorsque les lemmings sont en mesure de se reproduire. Les refuges d'hiver des arvicolinés étaient fortement associés aux restes de neige au printemps, ce qui indique que les lemmings choisissent surtout les zones à forte épaisseur de neige. Des températures très basses à l'automne et une couche de neige peu profonde semblent être d'importants facteurs limitants pour les lemmings en hiver et peuvent éventuellement prolonger la période de faible densité des populations de *Dicrostonyx*.
[Traduit par la Rédaction]

Introduction

Collared lemmings (*Dicrostonyx* spp.) experience winter conditions for at least 8 months of the year and display various adaptations to these conditions. In autumn they change from summer morphology, with dark pelage, to winter morphology, with greater mass, more rounded body shape, longer gastrointestinal tract, thick white outer fur, and bifid claws on the forepaws (Hansen 1957; Mallory et al. 1981, 1986; Malcolm and Brooks 1985, 1993; Reynolds and Lavigne 1989). These changes significantly improve the lemmings' energy metabolism and conservation (Scholander et al. 1950; Chappell 1980; Reynolds and Lavigne 1988, 1989; Malcolm and Brooks 1993). In addition, lemmings build subnivean nests of dead vegetation, critical for winter survival and reproduction (MacLean et al. 1974; Chappell 1980; Casey 1981), and choose areas of deepest snow as winter habitat because snow moderates low ambient temperatures through early winter and midwinter (MacLean et al. 1974; Fuller et al. 1975*a*; Chappell 1980).

Lemmings breed under the snow virtually every spring (April and May), but they may not breed every winter (November through March) (Krebs 1964; Fuller et al. 1975*b*). Weather and snow conditions may limit winter and spring breeding. Population growth to peak densities, resulting from successful winter reproduction, coincides with relatively warm and snowy early-winter conditions (Shelford 1943), and autumn conditions without freezing rain followed by relatively heavy early winter snow (Krebs 1964; Scott 1993). Higher spring temperatures may favour spring breeding by quickly melting snow that keeps the subnivean space colder than the ambient temperature (Fuller et al. 1975*a*; MacLean et al. 1974).

Lemming populations do not increase in all winters with apparently suitable snow and temperature conditions (Krebs 1964; MacLean et al. 1974), perhaps because of predation, especially by ermine (*Mustela erminea*) and least weasels (*M. nivalis*) (Maher 1967; MacLean et al. 1974).

At Pearce Point, Northwest Territories, collared lemmings stayed at low densities (<3/ha) for 6 years and bred in spring

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(April or May) under the snow, and perhaps earlier in the winter, in six consecutive winters (Krebs et al. 1995; Reid et al. 1995). Breeding often allowed populations to recover from summer declines driven principally by predation mortality, but in some winters populations declined (Krebs et al. 1995; Reid et al. 1995). We are interested in understanding why populations do not increase enough in winter to exceed the ability of predators to limit their population growth in the subsequent summer.

In this paper we first estimate the reproductive effort required to achieve observed rates of winter population change at Pearce Point. Second, we investigate the role of ermine predation. Third, we assess whether wintering microtines use habitats with the deepest snow. Fourth, we assess how much of the variance in rates of population change in winter can be explained by a combination of (*i*) cold stress during the autumn moult and change in morphology (September and October), (*ii*) thermal conditions under the snow (a combined function of ambient air temperature and snow depth) during winter breeding (November through March), and (*iii*) snow depth during spring breeding (April and May).

Methods

Study area

The study took place at Pearce Point (69°48′N, 122°40′W) on the south shore of Amundsen Gulf, on the western mainland of the Northwest Territories, Canada. The coastal tundra comprises dry *Dryas–Carex* heath, mesic *Carex–Salix–Dryas* hummock (frost-boil), and wet *Carex* meadow vegetation communities, all within 20 m asl.

The following climate data are from maps in Maxwell (1980), based on years 1941–1972. Pearce Point lies close to the 100-cm isohyet for annual mean total snowfall. The mean date of snow cover formation is October 1, but snow cover can be delayed until November 1. Monthly snowfall is highest in September (17 cm), October (22 cm), and April (12 cm). However, mean snow depth at the end of October is only 5–10 cm because of autumn melting. Mean snow depth reaches 20 cm by the end of November and 25 cm by the end of January, but stays at that depth until a rapid melt in May. The mean daily temperature is approximately 2°C in September, −27.5°C in January, and −5°C in May.

Climate data

Mean daily temperature and daily snow depth were measured at the Department of National Defence radar base at Clinton Point (69°35′N, 120°48′W), approximately 65 km east of Pearce Point, at 101 m asl, but also close to the coast. Data were made available by the Atmospheric Environment Service of Environment Canada. We use these data to represent winter conditions at Pearce Point, since we lack winter data from the study area itself. Long-term climate data (Maxwell 1980) indicate that conditions at Clinton Point are very similar to those at Pearce Point.

To estimate the effect of temperature and snow depth on lemming population growth, we derived three indices of thermal stress corresponding to three time periods with differing intensities of reproduction by lemmings (Krebs 1964). *Autumn cold stress*: we used the mean of all mean daily temperatures for September and October as an index of the cold stress lemmings encounter while changing from summer to winter morph, during which time they rarely breed. Although morphological changes can be induced by decreasing the photoperiod to light availability of less than 25% of the day (Hasler et al. 1976; Malcolm and Brooks 1985; Reynolds and Lavigne 1988), the role of lower temperatures is unknown. Between August and November the sunlit proportion of the day at Point Barrow, Alaska (71°N), decreases from 65 to 20%, reaching a mean of 9% for November (Chappell 1980). September and October are therefore the critical months for photoperiod-induced changes in morphology. *Winter cold stress*: during winter (November–March), when lemmings can breed under the snow, we calculated an index of cold stress as the sum of all daily snow depths over the period, divided by the sum of mean daily temperatures over the period. Since all mean temperatures were below freezing, this gave the ratio of centimetre-days of snow to degree-days of frost. Higher index values actually reflect lower stress under the insulative blanket of snow. *Spring cold stress*: during spring (April and May), when lemmings frequently breed, we estimated the insulative power of the snow as the mean daily snow depth over the period.

Estimation of population density

We estimated population densities of collared lemmings and tundra voles (*Microtus oeconomus*) using mark–recapture and the open Jolly–Seber population model. Animals were caught alive in Longworth traps and individually identified with numbered ear tags. Densities were estimated on four grids, each 18–25 ha, from early June to late August in each of six summers (1988–1992). One grid was maintained as a predator exclosure (PE) in summer (Reid et al. 1995). However, this exclosure did not keep out mammalian predators in winter because drifting snow allowed red foxes (*Vulpes vulpes*) to enter over the fence and ermine could get through the fence. We therefore consider PE an untreated grid for the winter. For details on trapping and population estimation see Krebs et al. (1995) and Reid et al. (1995).

We did not measure birth and death rates during the winter. Instead we use instantaneous rates of population change, calculated from changes in lemming densities from late one summer to early the following summer, as a composite measure of demographic processes, and therefore of population growth. Instantaneous rates are presented on a weekly basis because the time elapsed between late- and early-summer density estimates differed between years by a few weeks.

Lemmings were classified as subadults or adults on the basis of prominent changes in pelage with maturity. At snowmelt in spring, those with subadult pelage were classified as spring-born (born under the snow in April or May); those with adult pelage were classified as overwintered adults, surviving from the previous summer or having been born during the winter (November–March).

To estimate how many winter litters were necessary to explain the population changes observed between summers, we used a simple difference equation model with three time periods corresponding to the stress indices: autumn, winter, and spring. We considered only females of two age-classes, adult (≥35 g) and subadult. We lacked data on numbers of subadult females in early autumn, but assume that they were at least as frequent as adults. We assumed that each nest occupied by ermine represented the death of at least one female lemming. We assumed a winter litter size of three, based on embryo and corpora lutea counts presented by Krebs (1964) and a 50:50 sex ratio of neonates.

Winter snow distribution

In late May we mapped the distribution of remaining snow patches on some study grids (on PE, C1, and C2 in 1991; on PE and C2 in 1992). We assumed that this remnant snow coincided with areas of deepest snow during the winter. This was reasonable because most remnant patches were in the lee of hills or banks where snowdrifts form. Drifted snow is relatively dense because wind-blown crystals break and pack tightly in drifts (Kind 1981). Deep, dense snow melts relatively slowly because the upper layers insulate the lower layers from higher air temperatures, and compact, fine-grained

Table 1. Numbers of females on study grids in late summer (end of August) and early in the subsequent summer (early June), and minimum numbers of females killed by ermine during winter.

Grid	Late summer (adult females)	Early summer of the following year		Minimum no. of females killed by ermine (i.e., no. of nests occupied)
		Overwintered females	Spring-born females	
		Winter 1990–1991		
PE	8	6	6	5
C1	4	6	2	4
C2	3	7	5	3
C3	2	3	4	3
Total	17	22	17	15
		Winter 1991–1992		
PE	11	0	3	0
C1	1	0	0	3
C2	2	0	0	1
C3	1	0	1	2
Total	15	0	4	6

snow reflects a high proportion of incoming radiation (Male and Gray 1981).

Microtine winter nests

We estimated the density of microtine winter nests by systematically searching grids and plotting nest locations in early summer, immediately after snowmelt (PE, C1, C2, and C3 in 1991; PE and C2 in 1992). In 1992 we did not search C1 and C3 systematically, so we cannot estimate nest density. However, we did collect other information on all nests encountered during other activities on C1 and C3 in 1992. We were unable to differentiate lemming nests from those of voles.

Weasels line nests they occupy with fur from their rodent prey, and leave scats and prey remains nearby (Maher 1967; MacLean et al. 1974). The only *Mustela* species in the study area was the ermine. Each nest was examined for signs of occupancy by ermine, and the vicinity was searched for scats and remains (typically stomachs, feet and tails). All nests with ermine sign were removed to search them for prey remains and ear tags. All other nests were destroyed to avoid recounting them the subsequent year.

The association of winter nests with deep snow was tested by comparing the actual distribution of nests, either under snow or in the open in late May, with a random distribution. The random distribution assumed numbers in proportion to the percentage of ground either covered by or clear of snow in late May.

Results

Extent of winter breeding

We used data from 1990–1991, a winter of population growth, and 1991–1992, a winter of decline, to estimate the extent of winter breeding. The number of overwintered adult females in spring 1991 was higher than the number of adults late the previous summer on three of four grids (Table 1). However, only one ear-tagged adult female from summer 1990 was found on any of the grids in spring 1991. Evidently nearly all late-summer adults failed to survive the winter, so nearly all overwintered adults in spring had been born late the previous summer or in winter.

To assess how many litters may have been born in winter, we contrasted low- and high-survival scenarios using 1990–1991 data from grid C2, the grid with the highest rate of increase and only lemmings present (Table 1). In a low survival scenario we assumed only one subadult female for each adult in late summer and monthly survival rates of 0.6, 0.7, and 0.8 for autumn, winter, and spring, respectively. The adults surviving through autumn to winter would have to produce at least three litters to reach the numbers observed in early summer 1991. In a high-survival scenario, with two subadults for every adult in autumn and monthly survival rates of 0.8, 0.9, and 0.9 for autumn, winter, and spring respectively, early-summer numbers could be explained with only one winter litter per female. These latter survival rates are quite high for microtine rodents, so it seems likely that the strongest population growth from summer to summer is the result of multiple litters in winter, as well as spring reproduction.

During the 1991–1992 declines, there may have been little or no winter reproduction, but some lemmings survived to breed in spring. We found only spring-born lemmings in early summer 1992, indicating that the few adults that survived winter died during the spring.

Ermine predation

There was no significant difference between 1990–1991 and 1991–1992 in proportions of nests occupied by ermine (Mann–Whitney test, $U_s = 11.5 < U_{0.10}$), although all lemming and vole populations grew in winter 1990–1991 but declined in winter 1991–1992 (Table 2).

The instantaneous weekly rate of population growth was not significantly correlated with the percentage of nests occupied by ermine ($r = 0.21$, $F = 0.28$, $P = 0.62$) when data for both years were assessed together. For winter 1990–1991 there was a trend towards lower rates of population growth on grids with a higher percentage of nests occupied ($r = -0.75$, $F = 2.55$, $P = 0.25$). The trend was statis-

Fig. 1. Profiles of mean weekly snow depth over the 9-month periods of winters 1987–1990. Data were collected at Clinton Point, 65 km east of the study area.

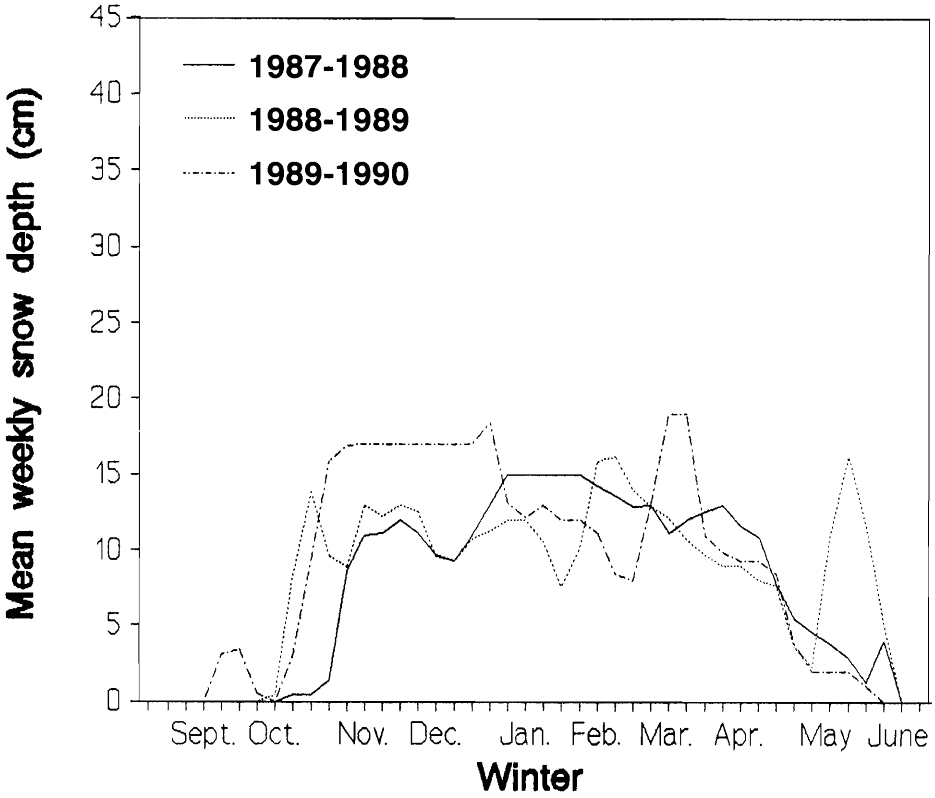


Table 2. Mean instantaneous weekly rates of population growth for microtines, microtine nest densities, and nest occupancy by ermine on the four study grids over two winters of intensive study (1990–1991 and 1991–1992).

	1990–1991	1991–1992
Instantaneous weekly rate of growth		
Both microtines	0.0221 (0.0090)	−0.0335 (0.0236)
Dicrostonyx only	0.0243 (0.0108)	−0.0327 (0.0149)
Microtine nests		
Nest density (no./ha)	2.69 (0.30)	3.13 (0.26)
Percentage occupied by ermine	7.6 (0.96)	5.3 (2.99)
Microtine remains		
Minimum no. killed as a proportion of the autumn population	0.72 (0.12)	0.08 (0.08)

Note: Numbers in parentheses are standard errors. Surveys of C1 and C3 were incomplete in 1992, so nest densities are based on two grids.

tically insignificant, perhaps because the number of data points was small.

Nest distribution

Winter nests were positively associated with areas of deepest snow accumulation on all three areas assessed in 1991 (PE: $G = 83.71$, $P < 0.001$; C1: $G = 24.41$, $P < 0.001$; C2: $G = 19.05$, $P < 0.001$) and on one of two areas in 1992 (PE: $G = 17.44$, $P < 0.001$). The insignificant association on C2 in 1992 ($G = 0.89$, $P > 0.10$) may have resulted from a late snowmelt and our mapping of snow cover before many areas of thin snow had melted.

Snow and temperature regimes

Snow-depth profiles for the five winters studied (Figs. 1 and 2) generally followed the pattern found in long-term climate data (Maxwell 1980). Most September snowfalls melted, but snow accumulated rapidly in late October and early November, after which it was relatively stable for the rest of the winter. However, snow depths towards the end of January were all below the long-term mean, 25 cm (Maxwell 1980). Only in 1990–1991 did snow depths exceed this level in late winter.

Dicrostonyx populations grew in three of five winters and declined in two, and the indices of thermal stress varied

Fig. 2. Profiles of mean weekly snow depth (cm) over the 9-month periods of winters 1990–1992. Data were collected at Clinton Point, 65 km east of the study area.

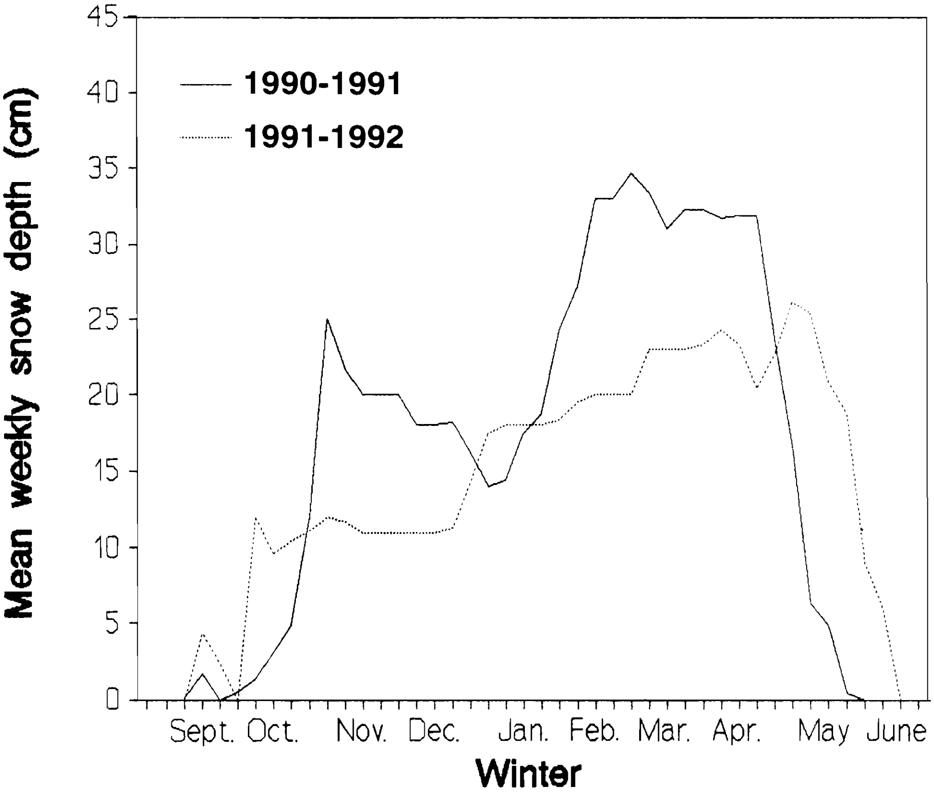


Table 3. Mean instantaneous weekly rates of population change (r) from late August to early June for *Dicrostonyx* alone on four study grids, combined with three indices of thermal stress that might affect r.

	r	Index of thermal stress[a]		
		Autumn	Winter	Spring
1987–1988	0.0326[b] (0.0131)	−0.66	0.627	6.4
1988–1989	0.0151[b] (0.0075)	−1.41	0.521	8.6
1989–1990	−0.0092[b] (0.0073)	−2.38	0.579	5.0
1990–1991	0.0243 (0.0108)	−2.82	0.926	15.0
1991–1992	−0.0327 (0.0149)	−4.45	0.720	20.8

Note: Numbers in parentheses are standard errors.

[a] Autumn, the average of the mean daily temperatures (°C) for September and October; winter, the cumulative centimetre-days of snow cover divided by the cumulative degree-days of frost for November through March; spring, the mean daily snow depth.

[b] Data from Krebs et al. (1995).

substantially between years (Table 3). The autumn stress index explained the highest proportion of variance in rate of change ($r^2 = 0.67$, $F = 6.124$, $P = 0.09$) (Fig. 3). When the index of thermal stress in winter was combined with the autumn index, the explained proportion of variance in rate of population change increased substantially ($r^2 = 0.98$, $F = 41.09$, $P = 0.02$). The addition of the spring index of thermal stress increased the explanatory power of the model only marginally ($r^2 = 0.99$, $F = 21.72$, $P = 0.16$).

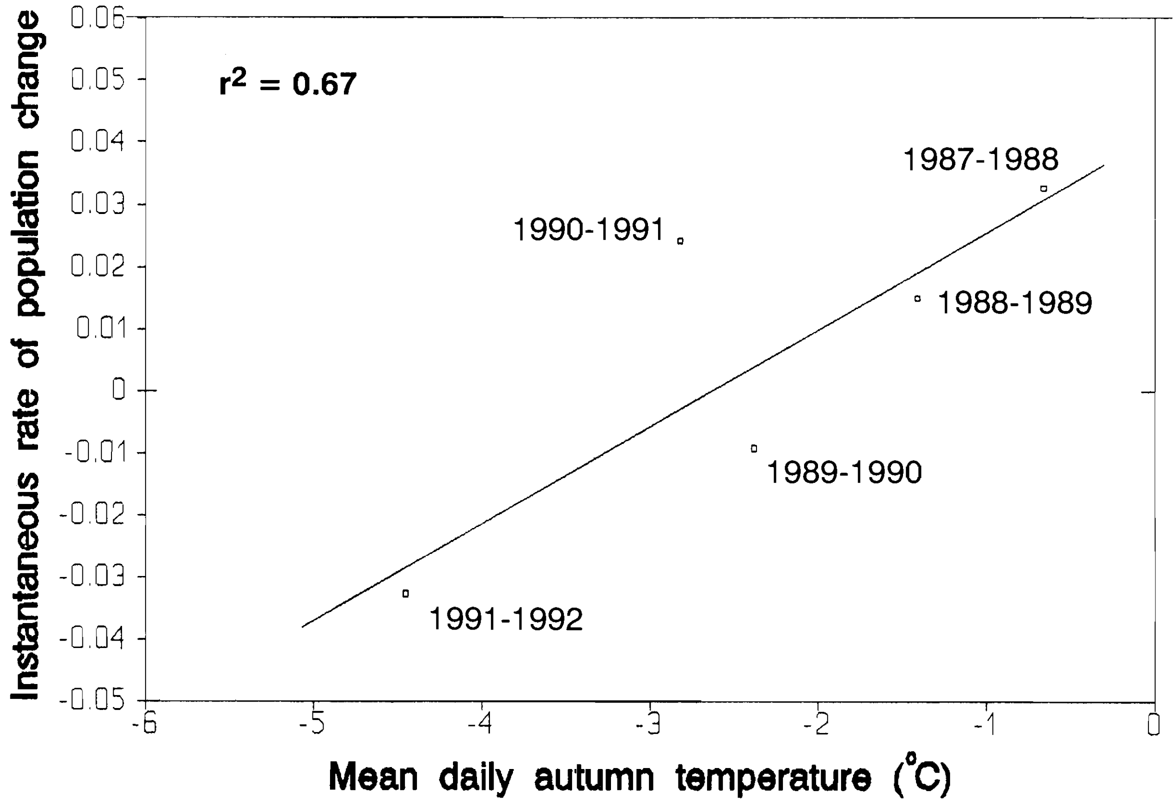
If these correlative data reflect causal processes, the intensity of cold in autumn appeared to have lasting effects on population growth in some winters. The autumn of 1991 was the coldest of five, and was followed by the steepest population decline (Fig. 3). The autumns of 1987 and 1988 were the mildest, and subsequent winters had high rates of population growth. However, cold autumns can apparently be ameliorated or exacerbated by thermal conditions during winter. For example, average population growth in 1989–1990 was less than expected, based on autumn temperatures (Fig. 3), perhaps because there was little snow in winter (Table 3, Fig. 1). By contrast, growth in 1990–1991 was higher than expected, based on autumn temperatures (Fig. 3), perhaps because of thick snow (Table 3, Fig. 2).

Discussion

Ermine predation

Our data on ermine predation in winter are very limited and any conclusions remain speculative. The intensity of ermine predation did not correlate well with winter population growth of microtines when winters were considered together, but within a winter of relatively good thermal conditions (1990–1991) there was a fairly strong inverse correlation. Perhaps the negative effects of cold and low snow cover on lemming survival and reproduction mask a potential limiting effect of ermine predation in a compensatory fashion, or directly compromise ermine survival (Brown and Lasiewski 1972).

Fig. 3. Relationship between instantaneous weekly rate of population growth over winter and the average of the mean daily temperatures during the autumn (September and October), when *Dicrostonyx* spp. are changing from summer to winter morphology.



Red foxes are the dominant predator at Pearce Point in summer and are present for at least part of the winters (Reid et al. 1995). They act as semigeneralists in this system, and are likely critical to maintaining lemmings at low densities (Reid et al. 1996). Fox predation in winter may obscure any relationship between ermine predation and lemming population growth.

A strong numerical response of ermine or least weasel, and therefore heavier predation, may occur following an irruption of a microtine population, as indicated theoretically (Hanski et al. 1993) and empirically (Fitzgerald 1977; Korpimaki et al. 1991; Korpimaki 1993), and as suggested by high rates of nest occupancy (16–34%) by *Mustela* spp. in association with lemming declines (Maher 1967; McLean et al. 1974; Fuller et al. 1975*a*). Lemmings did not irrupt at Pearce Point, and the ermine population apparently varied little between years (Reid et al. 1995). The proportion of lemming nests occupied by ermine at Pearce Point was consistently lower than maximal rates elsewhere, probably because ermine populations did not fluctuate dramatically.

Snow distribution

Distribution of lemmings among habitats in winter was strongly influenced by distribution of snow, as previously observed (Maher 1967; MacLean et al. 1974; Fuller et al. 1975*a*). Wind redistributes snow in drifts, and may keep upland tundra bare or thinly covered. Areas with little or no snow cover are poor winter habitat because of high energy costs and predation risk for lemmings foraging in the open.

Snow distribution, if it varies little between winters, probably cannot explain much of the variance in the rate of population growth within a study area. However, it may explain differences between regions with differing annual snowfalls. Within the range of *Dicrostonyx* spp., annual mean total snowfall varies from less than 50 cm to greater than 200 cm, and mean snow depths in late October from 5 to 50 cm (Maxwell 1980). Pearce Point has relatively little snow, on average (ca. 100 cm/year, and 5–10 cm at the end of October, Maxwell 1980), so the limiting effects of snow distribution and depth may be more pronounced here than in eastern regions, where snow is deeper (Maxwell 1980).

Hansson and Henttonen (1985) proposed that deep snow precludes successful foraging by generalist predators such as red foxes, thereby enhancing winter survival of rodent prey. Lindstrom and Hornfeldt (1994) found that small rodent prey constituted smaller proportions of fox diets as snow depth increased. The relatively shallow snow at Pearce Point may provide foxes with more hunting opportunities than are available in regions with deep snow.

Winter temperature regimes

The association of strong population growth with relatively deep snow, especially in November and December, has been noted before (Krebs 1964; MacLean et al. 1974; Scott 1993). However, combining snow depth with ambient air temperature is a useful index of thermal stress because it relates directly to the energy costs faced by lemmings under the snow.

A limiting effect of autumn cold is plausible, given the increased metabolic costs faced by summer morphs exposed to freezing temperatures (Chappell 1980; Reynolds and

Lavigne 1988). Autumn cold might affect population growth in a number of ways. First, higher metabolic costs induced by cold should force summer morphs to spend more time foraging, making them more vulnerable to autumn predation. Second, higher metabolic costs may diminish energy for body growth after maintenance requirements have been met, especially for late-summer young shifting to winter morphology. This is critical, since growth to a larger body mass and more rounded body shape are adaptive for energy conservation (Malcolm and Brooks 1993) and for reproduction in low temperatures (Collier et al. 1975). Third, in severe cold, maintenance energy requirements may not be met, and lemmings may die of exposure. We have no data to address these mechanisms, but suspect that the third is rare and the second most likely.

Duration of snow cover in spring was not strongly associated with our composite measure of winter population growth. The number of females breeding in spring and their individual reproductive efforts likely depended on their individual histories in autumn and winter, which may have overshadowed relationships in spring. Our study did not include years with benign autumn and winter conditions followed by a spring of long-lasting snow. In addition, lemming energetics and reproduction in spring are likely affected by changes in the thermal properties of snow, and by meltwater accumulations in burrows and lowlands.

Other factors affecting winter population growth

The frequency and dispersion of foods could influence population growth because of the role played by distance travelled and time spent away from the nest in female reproductive success (Collier et al. 1975). Winter food availability presumably increases as more tundra is covered in snow, but we do not know how snowfall relates to snow distribution. We can only say that food availability may have been a limiting factor at Pearce Point in any of the winters studied. We recommend quantifying standing crops of lemming foods and snow distribution in any attempts to explain regional variation in rates of winter population growth.

Mallory et al. (1986) proposed that age structure may influence winter reproductive potential; lemmings born in spring and surviving the summer may not acclimate to winter as well as summer-born young, so an autumn population with a high proportion of older individuals may have relatively low rates of survival and reproduction. We cannot address this idea adequately because we lack data on recruitment of late-summer young as autumn adults. A young age structure following a summer of population growth may enhance winter population growth (Mallory et al. 1986), but only if autumn cold does not impede growth to optimal body size for winter reproduction.

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