

Limitation of collared lemming populations during a population cycle

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Collared lemmings (*Dicrostonyx groenlandicus*) fluctuate cyclically in abundance on the Kent Peninsula, Northwest Territories, Canada. We tested whether predation was a necessary limiting factor of the lemming population in summer during the peak and decline phases (1996 and 1997) of the cycle. We reduced predation by means of a fence and an overhead mesh of monofilament line over 11 ha, completed late in the summer of the increase phase (1995). We used mark-recapture and radio-telemetry to investigate differences in demography between this predator enclosure and three control areas. Neither proportions of reproductive animals, nor sex ratio, nor net distances moved between trapping sessions differed significantly between the Enclosure and Controls. Adults were larger in the Enclosure than on Controls throughout the experiment; female juveniles born in the first summer litter of the peak were also larger within the Enclosure by August. Density was much higher in the Enclosure than on Controls in both 1996 and 1997. While density declined in 1997 on Controls, it first declined but then rose in the Enclosure; hence the population decline was reversed within the experimental area. Most mortality was due to predation in all three summers, but survival was significantly higher within the Enclosure only in the decline phase. We conclude that predation was necessary to limit the population in the peak and decline summers, but that the magnitude of the limitation was greater in the decline. Our results demonstrate that predation depresses peak and minimum densities of *Dicrostonyx* and further shapes the population cycle by extending the duration of the decline.

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Populations of collared lemmings (*Dicrostonyx* spp.) exhibit multi-annual fluctuations in many circumpolar regions. This pattern has been documented for *D. torquatus* on the Taimyr Peninsula (Dorogov 1983) and Wrangel Island (Chernyavski 1979), *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 1964a), near Igloolik (Rodgers and Lewis 1986), on Devon Island (Fuller et al. 1975b), on the north slope of Alaska (Batzli et al. 1980), in the Central Northwest Territories (Poole and Boag 1988, Cotter 1991, Wilson and Bromley unpubl.), and in Greenland (Sittler 1995).

An exception is the population of *D. g. kilangmiutak* at Pearce Point in the Northwest Territories (Krebs et al. 1995, Reid et al. 1995) that maintains persistent low densities. Where other sympatric microtines occur, including Siberian lemmings (*Lemmus sibiricus*), brown lemmings (*L. trimucronatus*), red-backed voles (*Clethrionomys rutilus*), and tundra voles (*Microtus oeconomus*), they tend to cycle synchronously with *Dicrostonyx*.

Predators respond (Solomon 1949) numerically (Maher 1967, 1970, Pitelka 1973, MacLean et al. 1974, Batzli et al. 1980, Henttonen et al. 1987, Underhill et al. 1993) and functionally (Reid et al. 1997; and see Batzli

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et al. 1980) to increases in lemming numbers. Because the increase in numbers of predators may lag the increase in lemming density, delayed density-dependent predation is one of many hypothesised causes of population cycles in lemmings (Stenseth and Ims 1993), as in other microtines (Taitt and Krebs 1985). Even if predation does not cause the cycle, it may limit (reviewed by Sinclair 1989) prey density, resulting in reduced peak densities, accelerated declines, and extended periods of low density (Taitt and Krebs 1985). However, if other causes of mortality compensate sufficiently (Errington 1946), predation may not be limiting. Also, if the population is limited by food or by spacing behaviour then any reduction in predation may be offset by changes in reproduction or emigration. On the other hand, predation may be limiting in only certain phases of the cycle – in the decline phase, for example, when the predation rate is expected to rise owing to a delayed numerical response of predators.

Radio-telemetry studies of microtines have revealed that a large proportion die proximately of predation (Brooks and Banks 1971, Heske et al. 1993, Krebs et al. 1995, Norrdahl and Korpimäki 1995a, Reid et al. 1995, Steen 1995; and see Steen et al. 1997). When predators have been experimentally excluded or removed, microtine numbers have usually, but not always, increased relative to control populations (Erlinge 1987, Desy and Batzli 1989, Reid et al. 1995, Korpimäki and Norrdahl 1998; cf. Marström et al. 1988, Norrdahl and Korpimäki 1995b). The sole experiment of this type on lemmings was that of Reid et al. (1995), who concluded that predation curtailed summer growth of a non-cyclic population of *Dicrostonyx*. Limitation by predation of a cyclic lemming population has not previously been studied experimentally.

By experimentally reducing predation on 11 ha of tundra and using radio-telemetry to determine the fates of collared lemmings (*D. g. kilangmiutak* Anderson and Rand), we tested whether and to what extent predation was necessary to limit the lemming population in the summer during the peak and decline phases of a cycle. A necessary condition is a prerequisite, a condition that must prevail for another to occur. Hence if predation is necessary to limit the population then reducing predation will cause density to increase. We tested the following predictions. If predation is a necessary limiting factor in summer, then (1) some mortalities must be due proximately to predation, and when predators are removed (2) density will increase, (3) survival will increase, (4) reduced predation will not be compensated for by increases in other sources of mortality, and (5) increased survival will not be negated by changes in other demographic factors such as emigration or reproduction.

Study site

This study took place at the Walker Bay field station on the Kent Peninsula, Northwest Territories, Canada (68°21'N, 108°05'W). The region is characterised by shallow tundra ponds and lakes separated by low-lying flat grassy areas, mud flats, sedge meadows, or moist broad hummocks (less than 20 m above sea level). Several ridges of higher land (less than 40 m a.s.l.) rise above the wet tundra; dens of arctic foxes and nests of owls and raptors are commonly situated on this high ground. Collared lemmings are most abundant in the hummocky habitats, where the predominant vegetation is *Salix lanata*, *S. arctica*, *S. reticulata*, *Dryas integrifolia*, and *Carex bigelowii*. Brown lemmings prefer wetter habitats dominated by sedges and grasses including *Carex bigelowii*, *C. salina*, *Eriophorum angustifolium*, and *Dupontia fisheri*.

Predators on lemmings in this region include arctic foxes (*Alopex lagopus*), ermine (also known as short-tailed weasels or, in Europe, as stoats) (*Mustela erminea*), arctic ground squirrels (*Spermophilus parryi*), parasitic, pomarine, and long-tailed jaegers (known in Europe as skuas) (*Stercorarius parasiticus*, *S. pomarinus* and *S. longicaudus*), short-eared owls (*Asio flammeus*), snowy owls (*Nyctea scandiaca*), rough-legged hawks (*Buteo lagopus*), glaucous gulls (*Larus hyperboreus*), sandhill cranes (*Grus canadensis*), common ravens (*Corvus corax*), and peregrine falcons (*Falco peregrinus*).

Methods

We trapped lemmings on four plots, each 300 m × 300 m (9 ha) (Fig. 1). The sites were at least 0.5 km apart and largely separated by ridges, ponds, or mud flats. We protected one plot from predators by surrounding it with a protective predator enclosure (approximately 11 ha). This plot was chosen because of its proximity to mud flats for delivery of building materials by plane and off-road vehicle, and was one to several m higher in elevation (≥ 10 m a.s.l.) than were the other plots (all < 10 m a.s.l.). The elevation change was not noticeable, but the Enclosure was one of two drier plots, with a greater area of dry land (not covered by ponds) than on two of the Control grids (Table 1). The plots were carefully chosen to be as similar as possible, so that the predominant habitat type was hummocks with willow and *Dryas* shrubs. We estimated the total area of shrubby habitat with both these genera present; most of the remaining habitat was dominated by sedges or grasses. The Enclosure plot comprised slightly more shrubby habitat than did the other plots (Table 1). We calculated all estimates of lemming density per ha of dry land on the grids (Table 1 and see below).

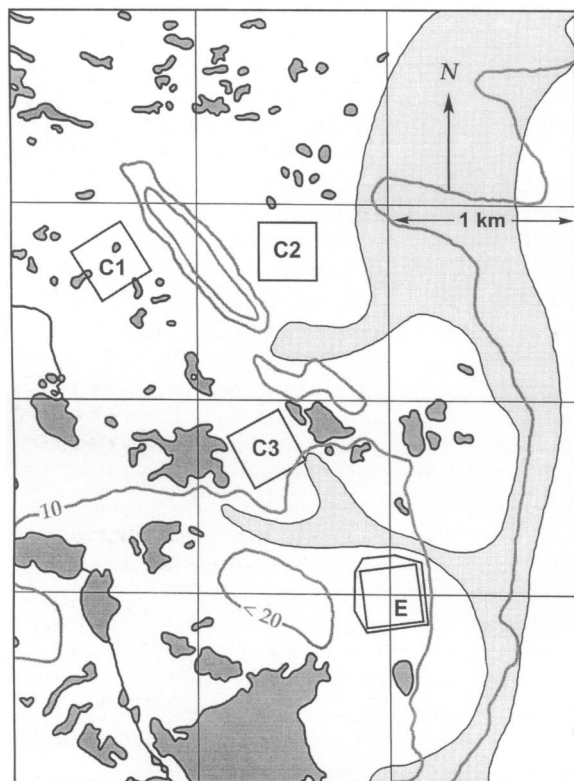


Fig. 1. Map of trapping grids at the Walker Bay field station, Kent Peninsula, N.W.T. used in 1994 through 1997. Control grids are indicated as C1, C2, and C3; the predator enclosure is labelled E and the surrounding fence is shown. Dark shading represents the largest lakes and ponds; light shading shows the approximate extent of mud flats. Contour lines show 10 m elevations and approximate locations of ridges of higher ground (< 20 m above sea level).

The protective enclosure consisted of a chicken wire fence to deter large mammalian predators and a cover of parallel lines of taut monofilament fishing line to deter avian predators. Lemmings could pass through the chicken wire (2.5 cm mesh size). The fence stood 1.5 m high; the monofilament was spaced approximately 45 cm apart, about 2 m above the ground. Reid et al. (1995) described a similar construction. The monofilament was completed by 27 July 1995. The fence was erected by 25 July 1995 and the 50-cm apron of chicken wire at its base was buried in soil by 8 August. It acted as a predator enclosure during the snow-free period.

The protected area was not designed to exclude ermine, but we have few records of these animals within

the enclosure. We found an apparently starved ermine in the enclosure when it was under construction in July 1995. In August 1996 we trapped and removed two ermine, and in August 1997 we saw one ermine in the enclosure. Arctic ground squirrels could have burrowed under the fence, but they tended to use drier habitats and were not observed on any of our plots. The structure effectively excluded avian predators in summer, but predation by arctic foxes occurred inside in August 1996 and June and August 1997; the foxes jumped the fence or sometimes chewed through it. The enclosure was less effective in winter – snow covered the fence and signs of arctic foxes and snowy owls were found within the area each spring.

On each plot we surveyed a trapping grid of 10 rows and 10 columns of wooden stakes 30 m apart. A Longworth trap was placed near an active burrow or in a runway near each grid point. The traps were left locked open on the grids during winter (since 1993 on Control plots and since 1994 on the Enclosure plot). Throughout the summers of 1994 and 1995 we trapped in one-day sessions (trapping in the Enclosure began in 1995). In 1996 and 1997 we trapped in two-day sessions whenever possible; on the second day traps were moved to a new location. We also caught lemmings that were sheltering in open traps when we cleaned traps during snowmelt each spring. Traps were baited with apple, shaded with wooden boards, and checked every five hours. We marked both collared and brown lemmings with numbered metal ear tags (fingerling tags). Of more than 1200 lemmings tagged in 1995 and 1996, only a few were recaptured in the subsequent year – all *Dicrostonyx*, two on Control grids and five in the Enclosure.

Because of limited staff, we were not able to trap on Control grid 3 in 1995 or late in 1997. As well, in 1995 and 1996 trapping sessions for the different grids could not be scheduled as close together in time as we would have liked. Analytical treatments of these problems are outlined below.

Estimation of density from mark-recapture data

We estimated the abundance and survival of *Dicrostonyx* in 1995 by means of the Jolly-Seber method (program JOLLY, Krebs 1989: 485). For the equivalent estimates in 1996 and 1997 we used the robust design method (Pollock 1982, Pollock et al. 1990) in program

Table 1. Approximate areas of dry land (land not covered by ponds) and shrubby habitat (hummocks dominated by willows and *Dryas*) on the four trapping grids used at Walker Bay, Kent Peninsula, N.W.T. in 1994 through 1997.

Grid	Control 1	Control 2	Control 3	Enclosure
Dry land (ha)	8.1	9.0	8.2	8.9
Shrub habitat (ha)	5.9	7.4	4.8	7.7
Shrub habitat as % of dry land	72	82	60	86

MARK (White 1998). (In 1995 our trapping sessions did not follow the robust design; the analyses performed by program JOLLY were equivalent to those now available in MARK for such data.) MARK computes maximum likelihood estimates of the parameters of models that predict the encounter histories of animals. The robust design model combines the Cormack-Jolly-Seber (CJS) (Cormack 1964, Jolly 1965, Seber 1965) open population mark-recapture model and models developed for closed populations (Otis et al. 1978). The robust design requires a sampling protocol in which primary trapping sessions each consist of multiple secondary sampling sessions close together in time. It is assumed that the population is closed within each primary trapping session (i.e. among secondary sessions within each primary session), and therefore data from each primary session are analysed with closed-capture models. Unlike the Jolly-Seber method, some of the closed-capture models allow unequal catchability among individuals; therefore they can provide improved estimates of capture probability and hence population size. Survival between the primary sessions can then be estimated with greater precision than is possible with the Jolly-Seber method alone. It is also possible to estimate probabilities of temporary emigration from, and re-immigration to, the study area.

Closed-capture models with only two secondary trapping sessions, as we had, cannot allow for a behavioural trap response (Otis et al. 1978). However, with a series of closed-capture sessions, MARK allows estimation of a temporary trap response. For each primary trapping session comprising two secondary sessions, MARK estimates three parameters: the probability of capture in the first secondary session (p_1), the probability of capture of an unmarked animal in the second secondary session (p_2), and the probability of recapture (c). Only two of these are estimable for one primary session, but they all can be estimated with multiple primary sessions under the realistic assumption of an additive relationship among the parameters over time – that is, that differences between p_1 , p_2 , and c are constant among the primary sessions. This model accommodates both a temporary trap response and time variation. It is possible to determine whether these parameters are needed by testing for differences among p_1 , p_2 , and c , as well as among primary sessions. Differences in trappability among groups of animals – among trapping grids in our case – can also be modelled. Other heterogeneity among individuals cannot be accounted for with only two secondary trapping sessions and can lead to underestimation of density; however, survival estimates are relatively insensitive to such variation (Pollock et al. 1990). A permanent trap response can bias density estimates in either direction, but does not affect survival estimates (Pollock et al. 1990). We assumed that any heterogeneity in the trappability of lemmings was consistent among grids, thereby introducing a constant bias.

Table 2. Procedure for testing increasingly parsimonious models of density and survival in MARK. If any step caused AIC_c (see text) to increase, it was omitted.

(1) Start with full model:	$c = x + p_2 = y + p_1(t * g)$ $N(t * g) S(t * g)$
(2) Set $p_2 = p_1$:	$c = x + p_2 = p_1(t * g)$ $N(t * g) S(t * g)$
(3) Set $c = p_2$:	$c = p_2 = p_1(t * g) N(t * g)$ $S(t * g)$
(4) Remove $(t * g)$ interaction from c , p_1 , p_2 :	$c = p_2 = p_1(t + g) N(t * g)$ $S(t * g)$
(5) Remove g and then t effects on c , p_1 , p_2 :	$c = p_2 = p_1(t) N(t * g)$ $S(t * g)$
	$c = p_2 = p_1(\cdot) N(t * g)$ $S(t * g)$
(6) Remove $t * g$ interaction from S (1997 model only):	$c = p_2 = p_1(\cdot) N(t * g)$ $S(t + g)$

Notation is as follows: N population density estimates; S survival estimates; p_1 probability of capture in first secondary trapping session; p_2 probability of capture in second secondary trapping session; c probability of recapture: the probability that an animal caught in the first secondary trapping session is recaptured in the second secondary session; t a time effect; g a trapping grid effect; $*$ an interactive effect: $(t * g)$ includes effects of t , g , and the interaction between t and g ; $+$ an additive effect: $(t + g)$ includes effects of t and g but no interaction; $\cdot$ a constant parameter; i.e. no variation among grids or times; $c = p_2 = p_1$, p_1 , p_2 , and c all equal; $c = x + p_2 = p_1$, p_1 and p_2 equal and the difference between these parameters and c constant among grids or times; $c = x + p_2 = y + p_1$ differences between p_1 , p_2 , and c constant among grids or times.

From the probabilities of capture and recapture described above, the robust design model estimates a capture probability parameter (p^*) for each primary trapping session. Other parameters estimated are N_i , the population density at the beginning of the i th primary session, and S_i , the probability of survival between primary sessions i and $i + 1$. Each parameter can be estimated separately for identified groups of animals (trapping grids in our case, next paragraph). We set the emigration and re-immigration parameters, γ'' and γ' , to 0 so that the survival parameters represented the same apparent survival estimated by the Jolly-Seber model – that is, the survival parameters included effects of emigration.

We used MARK to fit a series of increasingly parsimonious hypothetical models to the data of individual encounter histories (Table 2). From these we selected a model by minimising Akaike's information criterion (AIC) (Akaike 1974). AIC is calculated as $AIC = -2\ln(L) + 2p$, where L represents the maximised likelihood of the model, and p the number of parameters in the model. (MARK actually computes AIC_c , which corrects the bias introduced when the sample size is small relative to the number of parameters estimated.) AIC attempts to trade off bias against variability of estimates. As the number of parameters in a model increases, both the bias and precision of estimates tend to decrease. Therefore AIC penalises the increased likelihood of a better-fitting model by the number of

additional parameters required. Examples of successively simpler models of trappability in the first secondary session (p_1) are (1) non-additive (interactive) effects of time and trapping grid, abbreviated $p_1(t * g)$; (2) additive effects of time and grid, $p_1(t + g)$; (3) a time effect only, $p_1(t)$. In model $p_1(t * g)$ a separate trappability parameter is estimated for each grid and time period; therefore the number of parameters is $n_t \times n_g$, where n_t is the number of primary trapping sessions and n_g the number of grids. In model $p_1(t + g)$ the differences between parameters for each grid are constant at each time step; only $n_t + n_g - 1$ parameters are required, one for each trapping session and one each for the difference between the first and each other grid. In model $p_1(t)$ the parameters for all grids are equal but vary through time; only n_t parameters are needed. Similar sets of models can be built for other trappability (p_2 , c) and survival (S) parameters (Table 2). We found that likelihood ratio tests (White and Bennetts 1996) led to selection of the same model as did AIC_c. In these tests the fits of two nested models are compared by means of the ratio of their likelihoods, which follows a χ^2_d distribution where the degrees of freedom, d , equal the difference in the number of parameters between the two models.

In 1996 we trapped on two consecutive days on three occasions on each Control grid and on four occasions on the Exclosure grid. In order to compare among grids we grouped sessions on the four grids that were as close as possible in time. However, to avoid confounding density with time as the populations increased owing to summer reproduction, we ignored the last trapping session in the Exclosure (24–25 August) because it was later than sessions on the other grids. Our conclusions from this conservative procedure were the same as those reached if the last three rather than the first three sessions on the Exclosure were included. In 1997 we trapped on two consecutive days on four occasions on two Control grids and in the Exclosure. As in 1996, we grouped occasions for each of these three grids that were close in time. On the third Control grid there were only two trapping sessions, each of two consecutive days, in 1997. We estimated the densities on that grid by means of a closed-capture model under the same assumptions ($p_1 = p_2 = c$) made for the other grids in 1997. We calculated the densities of lemmings per ha of dry land on each grid (see above and Table 1), and used the adjusted t -test for comparing a single observation to the mean of a sample (Sokal and Rohlf 1995: 228) to compare an estimate for the Exclosure with the mean of the corresponding estimates for the Control grids at a particular time.

Survival estimation from mark-recapture data

In 1997 the time intervals between primary trapping sessions were similar among grids (Control 1: 13, 21, 22 d; Control 2: 13, 25, 20 d; Exclosure 14, 24, 21 d). Therefore we tested the null hypothesis that the survival rates in the Exclosure were equal to the survival rates of animals on the Control grids by comparing models generated in MARK, by means of likelihood ratio tests (White and Bennetts 1996). We compared the fits of three nested models all with survival (S) varying among the different time periods (t) between primary trapping sessions: (1) separate survival parameters for each grid ($S(t + g)$), (2) separate survival parameters for the Controls and the Exclosure ($S(t + \text{Excl})$), (3) equal survival on all grids ($S(t)$).

In 1996 the time intervals between primary sessions differed too much among trapping grids for us to be able to compare models. Instead we arithmetically converted the survival estimates from MARK into 14-d survival rates and 95% confidence intervals and compared them graphically among grids.

Survival estimation from radio-telemetry

We used radio-telemetry to obtain independent estimates of actual survival, by fitting a total of 214 adult and subadult lemmings with transmitters. We used Biotrack radio collars (SS1, SS2, and TW4) weighing approximately 3 g. No lemming received a radio weighing more than 10% of its weight. The position of each radio (a "fix") was recorded approximately every three days. If an animal could not be located, we searched extensively on and around the trapping grid and at known predator dens, nests and perches. When a dead lemming was found, the type of predator responsible was inferred from a necropsy, from the location of the radio, and from damage to the radio. Lemmings killed by arctic foxes had massive haemorrhaging under the skin or large puncture wounds, and were often found cached under moss or leaf litter. Foxes sometimes left only the stomach and radio but often dug up burrows or chewed collars. Ermine skinned their prey or ate the brain. Avian predators often left only the stomach and radio or a regurgitated casting containing the radio. We found transmitters and the remains of lemmings in fox dens, in ermine dens and near the nests of pomarine jaegers. Occasionally a dead lemming was found on or under the ground with no apparent injuries; we classified these as "non-predation mortalities". When possible, we removed or changed radios during the summer when batteries were due to fail. Most radio-collared animals that were alive at the end of each summer were recaptured and their collars were removed.

We estimated survival rates from the radio-telemetry data by means of Kaplan-Meier analyses with both singly-censored and progressively-censored (staggered-entry) data (Pollock et al. 1989). We plotted the survivorship function of animals in two groups, Control and Exclosure, in 1995, 1996, and 1997, and estimated their survival in June, July and August of each summer. Data from four animals that died within the first two days after radios were fitted were deleted because collars may compromise survival in the short term (Reid et al. 1995). Log-rank tests (Pollock et al. 1989; equivalent to Mantel and Haenszel's χ^2 test, Lee 1980: 136) were used to compare estimates between the Control and the Exclosure groups.

Reproductive activity

We weighed lemmings to the nearest 1 g and recorded their reproductive condition. We assigned them to weight classes according to their mass as follows: small (< 25 g), medium (25–49 g), and large ($\geq$ 50 g). They were additionally assigned to age classes based on their weight and pelage at first capture. Animals weighing $\leq$ 40 g at first capture were classified as born that season, either under the snow ("spring born") or in the first, second, or third summer litters, depending on the date of capture. Animals in juvenile or subadult pelage in May or June were classified as spring born regardless of their weight (usually < 40 g). All other lemmings weighing more than 40 g at first capture were considered adults.

A male was considered reproductive if his testes were scrotal, a female if her pubic symphysis was at least slightly open, her nipples enlarged, or she was obviously pregnant. To compare reproductive status among years, we chose four periods within each season that included, whenever possible, a trapping session from each year on the three main grids. We ignored data from the few trapping sessions outside these periods and from Control grid 3, where trapping was infrequent in 1995 and 1997. The relationship between reproductive condition and year, sampling period, and trapping grid was modelled by means of logistic regression (a generalised linear model for binomial data). This method uses an iterative weighted least-squares algorithm to estimate a maximum likelihood coefficient for each level of each factor (Statistical Sciences 1995: 8–27). The coefficient represents a transformation of the incremental probability that an animal at that factor level was in reproductive condition. Separate models were fitted for large, medium and small males and for large and medium females (no small females were classified as reproductive). In each case a parsimonious model was selected by eliminating terms that did not explain much variation in the response variable, according to Akaike's information criterion (AIC)

(Akaike 1974). Planned Helmert contrasts (Statistical Sciences 1995: 2–13) were used to compare the coefficient for the Exclosure with the mean of the coefficients for the Control grids. Planned "treatment" contrasts were used to compare other coefficients of interest: the peak year versus other years, and August versus other time periods. Functions "glm" and "step" in S-Plus (Statistical Sciences 1995) were used for these analyses.

Beginning in July 1996 we recorded oestrus (perforate vagina) as a separate indicator of female reproductive condition, but because of differences in assessments among field workers we could not compare rates of oestrus between years. Because the proportion of large animals in oestrus declined linearly throughout the 1996 season, the logistic regression for 1996 was modelled with trapping date as a continuous variable and grid as a discrete factor. A separate slope could therefore be fitted for each grid. We included in this regression the data from the last trapping session in the Exclosure in 1996 (24–25 August).

Sex ratio

We compared the proportion of male lemmings among years, sampling periods, weight classes and grids by means of logistic regressions similar to those described above. We grouped the trapping sessions in the same way as for analyses of reproductive condition.

Mass of adult and juvenile lemmings

We used a general linear model to compare the weights of adult animals of both sexes among years, sampling periods, and grids. A $\log_{10}$ transformation was applied to the data to normalise distributions and equalise variances. As above, AIC was used to identify a parsimonious model. We grouped the trapping sessions in the same way as for the analyses described above.

We wanted to compare weights of juvenile lemmings among grids after the juveniles had grown to adult size; the only cohort large enough for such a comparison was the first summer-born litter in 1996. We used models similar to those described above to compare the mass of these animals among grids in late July–early August when most were below 40 g and in August when most were above 40 g.

Movements of lemmings

As an index of distances moved by the lemmings on the different trapping grids, we calculated the net displacement between primary trapping sessions of lemmings caught in two successive sessions. The same trapping sessions were used for this analysis as for the above

analyses. A $\log_{10}$ transformation was applied to the data to normalise the distributions and the 95% confidence intervals for the mean displacements of males and females in each year were compared graphically. Most of the data were for large animals and none for animals weighing less than 25 g. The distances moved by animals of medium weight were similar to those moved by large animals, so we combined the two groups for these analyses. We also recorded the numbers of telemetered lemmings that moved away from the grid on which they were first captured.

Results

Abundance

In 1994 the density of lemmings was very low and we caught only two – a male *Lemmus* on 9 June and a female *Dicrostonyx* on 1 September. Nor were any lemmings trapped in 1994 in a snap-trapping survey conducted annually in July at Walker Bay (Wilson and Bromley unpubl.). We display estimates of 0.1 ha^{-1} (approximately 1 animal per grid) throughout 1994 (Fig. 2); otherwise data from the animals caught in 1994 are not included in the analyses reported below.

Jolly-Seber estimates of *Dicrostonyx* density in 1995 were approximately 2 ha^{-1} throughout the summer on all grids (Fig. 2) although 95% confidence intervals were large. Because the predator enclosure was not

Table 3. Successively parsimonious models from program MARK of 1996 *Dicrostonyx* density and survival. Models are sorted in increasing order of AIC_c (therefore the best model is first). Only the change in AIC_c (ΔAIC_c) relative to the best model is shown. Models are described using the notation shown in Table 2.

Model	ΔAIC_c	Parameters
1. $c = p_2 = p_1(t) N(t * g) S(t * g)$	0.0	23
2. $c = p_2 = p_1(t * g) N(t * g) S(t * g)$	3.2	32
3. $c = p_2 = p_1(t + g) N(t * g) S(t * g)$	4.0	26
4. $c = x + p_2 = p_1(t * g) N(t * g) S(t * g)$	4.4	33
5. $c = x + p_2 = y + p_1(t * g) N(t * g) S(t * g)$	4.7	34
6. $c = p_2 = p_1(\cdot) N(*g) S(t * g)$	7.8	21

completed until late July, we did not expect to detect differences in density or survival between the Enclosure and the Control grids.

In all our robust design models of density and survival, AIC_c was reduced ($\Delta AIC_c \leq -1.4$) by equating the probabilities of capture during the first secondary session (p_1), the second secondary session (p_2), and the probability of recapture (c) (Table 3, models 2, 4, 5). Therefore we assumed these parameters to be equal. In models of the 1996 data it was possible to assume that these parameters were also equal among grids ($\Delta AIC_c = -3.2$, Table 3, models 1–3). Because the time intervals between primary sessions differed among trapping grids in 1996, we did not try to equate survival parameters among grids. In models of the 1997 data we were able to assume no interaction between grids and time in the case of survival estimates ($\Delta AIC_c = -1.8$).

In early July 1996 the estimated density of *Dicrostonyx* was $8\text{--}11 \text{ ha}^{-1}$ on all grids (Fig. 2). In late July the estimated density in the Enclosure was nearly double the mean of the estimated densities on the Control grids (one-tailed t -test, $t_2 = 3.2$, $p < 0.05$). By mid-August the estimated density in the Enclosure was 34.1 ha^{-1} (95% c.i. $26.5\text{--}46.2$), more than double the mean of the estimates for the Control grids (16.4 ha^{-1} ; one-tailed t -test, $t_2 = 2.5$, $p < 0.07$).

During the winter of 1996–1997 the density of lemmings declined on all trapping grids. In mid-June 1997 the estimated density of *Dicrostonyx* was approximately $1\text{--}2 \text{ ha}^{-1}$ on two Control grids and 7 ha^{-1} on Control 1 grid and within the Enclosure (Fig. 2). On the Control grids the densities declined throughout the summer. The estimated densities on Control grids 1 and 2 in August, and on Control grid 3 in our last trapping session there in early July, were approximately 1 ha^{-1} or less (the largest 95% c.i. was $1.0\text{--}2.5$). Within the Enclosure, the density declined to about 3 ha^{-1} (95% c.i. $2.3\text{--}5.2$) by 1 July, but by August it rose to approx-

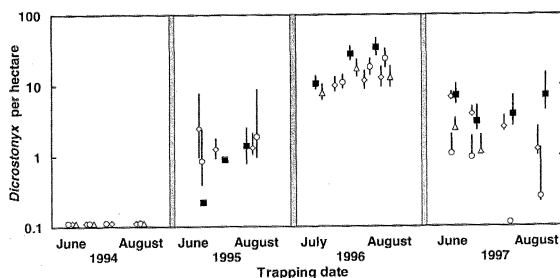


Fig. 2. Estimates and 95% confidence intervals of the population densities of *Dicrostonyx groenlandicus* on Control (diamonds, circles and triangles) and Enclosure (squares) grids, in 1994, 1995, 1996, and 1997. Density was estimated in 1995 by means of the Jolly-Seber method and in 1996 and 1997 by means of the robust design. Since in 1994 no *Dicrostonyx* were caught until August, arbitrary estimates of 0.1 ha^{-1} (approximately 1 animal per grid) were plotted. Densities are plotted on a logarithmic scale in order to (1) facilitate comparison of rates of population change by comparing the slopes of imaginary lines connecting two density estimates, and (2) allow the same Y-axis to be used for all years. Some confidence intervals in 1997 are very asymmetric, because MARK assumes a log-normal distribution of the number of animals not captured. Hence, although the lower bound of an estimate is defined by the total number of animals caught, the upper bound may be quite high (discussed for program CAPTURE by Rexstad and Burnham 1991). Points without error bars are those for which confidence intervals could not be estimated because of small sample sizes.

imately 7.2 ha^{-1} (95% c.i. 4.4–14.7). This estimated density in the Exclosure in August 1997 was 10 times that on the Control grids (0.7 ha^{-1} ; one-tailed t -test, $t_1 = 7.7$, $p = 0.04$). Hence, the decline was reversed in the experimentally treated area in summer 1997. The rate of change of density (r) was -0.19 per week on Control grids in summer 1997 and $+0.002$ per week in the Exclosure.

We caught few *Lemmus* except in 1996; in that year we caught few until July but they then increased in abundance on all grids. In 1996 there tended to be fewer *Lemmus* in the Exclosure than on the other grids; indeed there seemed to be an inverse relationship between the densities of the two species. The density of *Lemmus* remained lower than that of *Dicrostonyx* except that in mid-August on Control 1 grid the densities of the two species were similar. The increase of *Lemmus* on our study grids in the peak year may have been in part a result of emigration from overpopulated preferred wet sedge-grass habitats. Although *Lemmus* were most abundant on Control 1 grid, which had the largest area of wet habitat, they were caught in drier parts of the grids also. When the estimated densities of the two species in 1996 were summed (Fig. 3), the density of all lemmings in the Exclosure exceeded the mean on Control grids by 45% at the end of July and by 56% in mid-August (one-tailed t -tests, $t_2 = 4.0$, $p < 0.03$ and $t_2 = 2.7$, $p < 0.06$).

Survival estimates from mark-recapture data

During the period from late July to mid-August 1996, the 14-d survival rate of *Dicrostonyx* estimated from mark-recapture data was 50% higher in the Exclosure

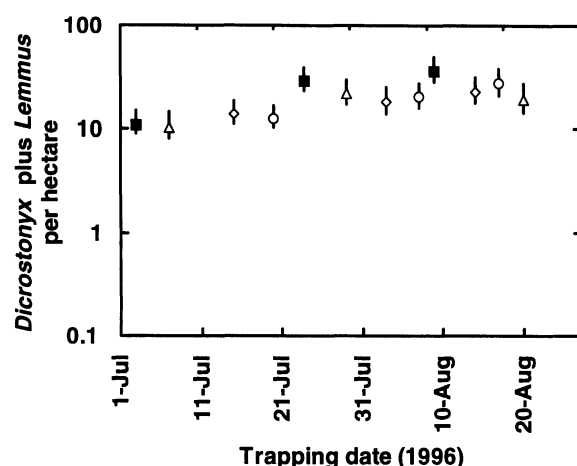


Fig. 3. Densities of both species of lemmings, *Dicrostonyx groenlandicus* and *Lemmus trimucronatus*, on Control (diamonds, circles and triangles) and Exclosure (squares) grids in 1996, obtained by summing estimates made separately for each species with the robust design.

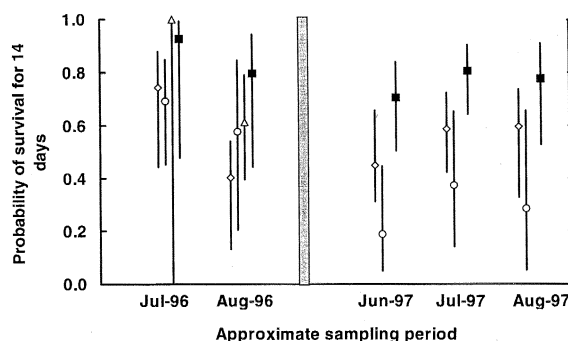


Fig. 4. Estimates and 95% confidence intervals from the robust design of the survival of *Dicrostonyx groenlandicus* on Control (diamonds, circles and triangles) and Exclosure (squares) grids, in 1996 and 1997. Survival was measured between the primary trapping sessions for which density estimates are plotted in Fig. 2.

than the mean of the estimates on Control grids (Fig. 4). The difference approached statistical significance (one-tailed t -test, $t_3 = 2.0$, $p < 0.09$), but the 95% confidence intervals overlapped considerably. Earlier in 1996 the survival rate in the Exclosure did not differ greatly from those on Control grids (Fig. 4). Throughout the summer of 1997, the survival rate of *Dicrostonyx* in the Exclosure, estimated with MARK, was roughly double the mean survival on Control grids in the three periods between primary trapping sessions. We rejected the null hypothesis that in 1997 survival in the Exclosure equalled that on Control grids because model $S(t)$, in which survival varied through time but was equal among grids, fitted the data far less well than model $S(t + \text{Excl})$, in which survival varied through time and differed between the Exclosure and Control grids ($\chi^2_1 = 8.8$, $p < 0.005$). Model $S(t + \text{Excl})$ fitted the data less well than model $S(t + g)$, in which survival differed among all grids ($\chi^2_1 = 3.8$, $p < 0.06$), showing that only part of the variation among grids was explained by the difference between the Exclosure and Controls. Survival estimates in 1995 from Jolly-Seber models are not reported here because these estimates had 95% confidence intervals spanning most of the range from 0 to 1. Survival rates of *Lemmus* could be estimated only in 1996 and were quite imprecise; the estimated survival of *Lemmus* within the Exclosure did not differ significantly from that on Control grids.

Survival estimates from radio-telemetry

We fitted 38 adult and subadult *Dicrostonyx* (weighing at least 28 g) with radio collars in 1995, 114 in 1996, and 62 in 1997 (Table 4). The lemmings were killed by arctic foxes in all three years, by ermine in 1995 and 1997, and by various avian predators (Table 4). We knew of five active natal fox dens within 5 km of our trapping grids in 1995, 10 in 1996, but none in 1994 or

1997. Predation by pomarine jaegers occurred only in 1996, when many bred in the study area. Predation on juvenile lemmings (reported below) by ermine occurred in 1996 on Control grid 1; a female ermine with seven young denned on the ridge nearby. Predation by ermine was heavy on the Control grids in 1997 but no known ermine predation occurred in the Exclosure in that year. This difference was most likely due to a patchy distribution of ermine, rather than to an Exclosure effect, since these animals could pass through the fence. We knew of a male ermine and a female with four offspring denning on the ridge between Control grids 1 and 2, but we were not aware of ermine in the Exclosure until August.

We recorded a lemming as "lost" when neither the individual nor its transmitter was ever found. Some of these losses may have been due to radio failure but probably most were due to predation, since the proportion lost was lower in the Exclosure by an amount similar to the reduction in the proportion killed by predators (next paragraph and Table 4).

In the three years respectively, 23%, 23%, and 49% of the telemetered lemmings were killed by predators on Control grids, compared with 9%, 16%, and 22% in the Exclosure (Table 4). The proportions of animals depredated, lost, and either alive or dead of unknown ("non-predation") causes (alive animals and non-predation mortalities were pooled because of small expected values for the latter) differed significantly between the Exclosure and Control grids only in 1997 (1995: $\chi^2_2 = 2.0$, $p > 0.3$; 1996: $\chi^2_2 = 3.9$, $p > 0.1$; 1997: $\chi^2_2 = 6.8$, $p < 0.05$). In 1996 and 1997 only about 9% of the

telemetered animals in the Exclosure died of causes other than predation, compared with less than 2% of Control animals. In 1996 the proportions of animals known to have died of all causes combined were approximately equal within (25%) and outside (24%) the Exclosure.

Although survivorship of adult and subadult *Dicrostonyx* (at least 28 g) estimated with Kaplan-Meier analyses of radio-telemetry data (Fig. 5) was generally higher within the Exclosure than on Control grids, the difference was significant in 1997 only (log-rank tests, 1995: $\chi^2_1 = 0.4$, $p > 0.5$; 1996: $\chi^2_1 = 0.3$, $p > 0.5$; 1997: $\chi^2_1 = 3.7$, $p < 0.054$). Even while the predator exclosure was under construction in 1995, it probably afforded some protection to the lemmings within. Predation events within the Exclosure are clearly apparent in Fig. 5, in July 1995 (by ermine), August 1996, and June and August 1997 (all by fox). Without the fox predation events, the difference in survival between the treatments in 1996 approaches significance ($\chi^2_1 = 3.3$, $p < 0.071$). Fourteen-day survival estimates were high (> 0.8) in each month of 1995 and 1996 in both treatments. In 1997 survival on Control grids fell from 0.94 (95% c.i. 0.87–1.0) in June to 0.75 (0.61–0.87) in July and 0.71 (0.27–1.0) in August. The estimated survival of animals on Control grids in 1996 exceeded that in 1997 by 14% (log-rank test, $\chi^2_1 = 5.2$, $p < 0.025$). The survival of Exclosure animals significantly exceeded that of Control animals (by 25%, log-rank test, $\chi^2_1 = 5.2$, $p < 0.025$) only in July 1997, when no known predation occurred within the protected area.

Table 4. Natural mortalities of adult and subadult radio-tagged *Dicrostonyx* (weighing at least 28 g) from the Control (C) grids and the Exclosure (E) in 1995, 1996, and 1997. Animals "alive when battery failed" were those that we were unable to recapture but were known to be alive and moving from radio fixes. "Lost" means both the radio and the lemming were never found. Not included are one animal in 1995 and three in 1996 that died within 2 d of being radio-collared. Also shown are the numbers of animals known to have moved at least 25 m from the edge of the grid on which they were first captured (in the case of the Exclosure, these animals went through the fence).

	1995		1996		1997	
	C	E	C	E	C	E
Animals radio-tagged	26	11	79	32	39	23
Still alive when radio removed or when battery failed	14	9	40	20	11	12
Lost	5	1	20	4	9	4
Mortalities due to predation	6	1	18	5	19	5
Fox or suspected fox	2	0	11	5 ^a	7	5 ^b
Pomarine jaeger			3	0		
Short-eared owl	3	0				
Unknown or suspected avian			4	0	1	0
Ermine or suspected ermine	1	1			10	0
Unknown predator				1	0	
Non-predation mortalities	1	0	1	3	0	2
% depredated	23	9	23	16	49	22
% non-predation mortalities	4	0	1	9	0	9
% total mortalities	27	9	24	25	49	30
% lost	19	9	25	13	23	17
Animals that left grid	2	0	3	1	5	2 ^c

^a all in August.

^b 4 on 28 June and 1 on 17 August.

^c one individual later re-entered the Exclosure.

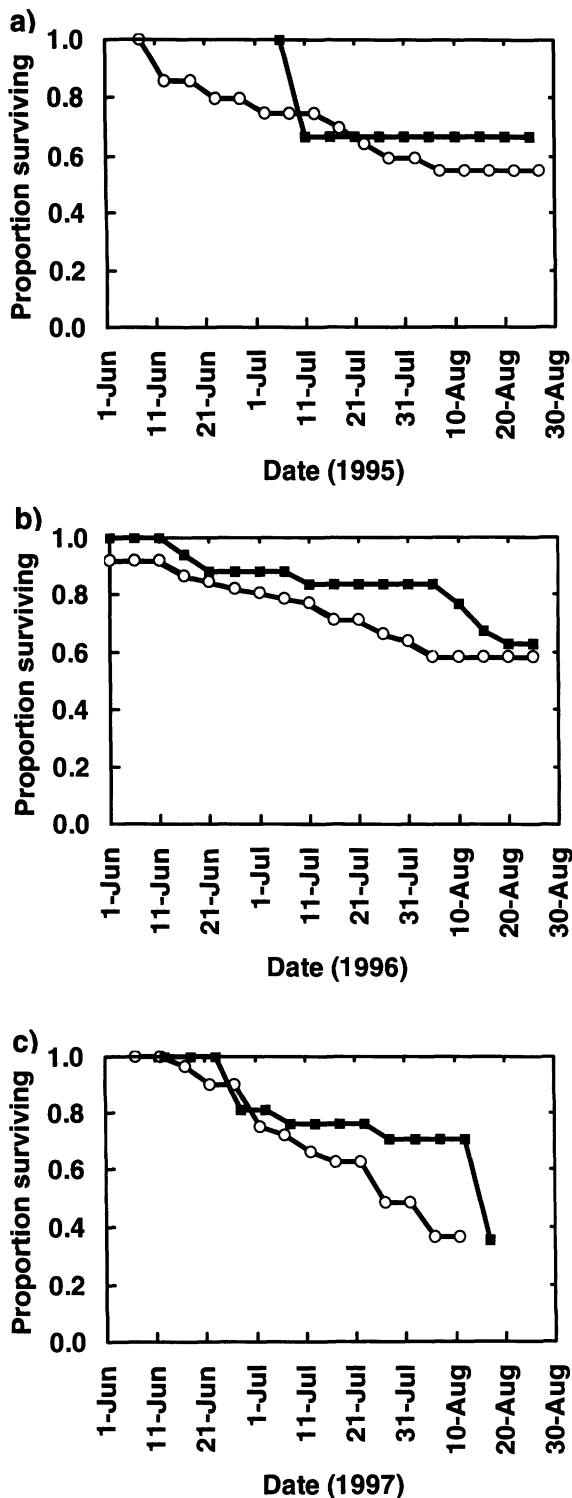


Fig. 5. Kaplan-Meier survivorship functions for telemetered adult and subadult *Dicrostonyx* (weighing at least 28 g) on Control (open circles) and Exclosure (filled squares) grids in (a) 1995, (b) 1996, and (c) 1997. In 1995, the first Exclosure lemming was telemetered on 6 July. The Exclosure was completed late in July 1995.

Comparison of results from the two methods

Analysis of our mark-recapture and radio-telemetry data led to different estimates of survival rates. The estimates from mark-recapture were generally lower and less precise than those from radio-telemetry, but mark-recapture estimates showed the improved survival in the Exclosure more consistently. All the instances when radio-telemetry estimates showed lower survival in the Exclosure than on Controls were associated with known predation events in the Exclosure. The differences between the estimates can be attributed to three main factors. First, the age classes of the two groups differed since we included all animals in mark-recapture estimates and only those at least 28 g in Kaplan-Meier estimates. Second, mortalities that occurred when few animals were telemetered had a large effect on the Kaplan-Meier estimates. For example, on 17 August 1997 one of the two remaining telemetered lemmings in the Exclosure was killed by a fox, resulting in a low, imprecise survival estimate for August even though it was the only mortality that month. Finally, as mentioned earlier we incorporated emigration into our mark-recapture survival estimates. In 1996 we observed little long-range emigration, but many animals caught early in the season were not recaptured later. At the high densities during the peak year our traps sampled only a small fraction of the population; therefore slight shifts in animals' home ranges, combined with our practice of moving traps to ensure random sampling, may have led to apparent emigration.

Reproductive condition – males

The factor "trapping grid" was not retained in the logistic models of reproductive condition for either large or medium-sized males ($\Delta AIC = -1.7$ and -3.7 , respectively); the only significant factors in these models were year and period. Further results of these analyses are presented in Wilson (1999). So few small males were in reproductive condition that we did not try to incorporate grid into the model for these males. Of 14 small males in 1996, five were caught in the Exclosure and one of these was reproductive. Of four small males in 1997, two were caught in the Exclosure and one of these was reproductive.

Reproductive condition – females

In the models of large and medium-sized female reproductive condition, the trapping grid term was retained. In the case of large females, differences among trapping grids in the proportion of females in reproductive condition were neither statistically significant ($t_{426} < 1.2$, $p > 0.2$) nor consistent among years or periods. The

proportion of medium-sized females in reproductive condition in the Exclosure exceeded the mean proportion on the other two trapping grids but the difference was not significant ($t_{183} = 1.6$, $p > 0.1$). We confirmed the lack of significance with a model incorporating all three Control grids in 1996 and 1997; the equivalent statistic was $t_{284} = 0.7$, $p > 0.4$. No small females were classified as reproductive.

Trapping grid was not retained in the models of female oestrus ($\Delta\text{AIC} < -2.5$) in either 1996 or 1997. Few medium-sized females were observed in oestrus: of 151 animals in 1996, four were in oestrus (two in the Exclosure and two on Control grids) and of 21 animals in 1997, one was in oestrus. No small females in oestrus were seen in any year.

Sex ratio

Trapping grid was not retained in the model relating sex ratio to year, period, and grid ($\Delta\text{AIC} < -0.18$); we conclude that the proportions of males and females did not differ significantly between the Exclosure and Control grids.

Mass of adults and juveniles

The average mass of animals classified as adults when first caught (weighing > 40 g) was greater in the Exclosure than on Control grids across all years (Fig. 6, $t_{697} = 9.9$, $p < 0.0001$). This pattern was true of both males and females ($t_{259} = 5.4$ and $t_{431} = 8.9$, $p < 0.0001$). The mean mass of males and females in the Exclosure across all years and periods was 68.9 g and 78.5 g, 12.6% and 19.1% higher than the corresponding mean weights on Control grids 1 and 2, 61.2 g and 66.0 g (calculated based on $\log_{10}$ transformed data). The model fitted the data well except that in June and early July 1995, before the protective structure was completed, observed mean weights of animals in the Exclosure were similar to the observed means on the Control grids and lower than the values estimated by the model for the Exclosure (Fig. 6a).

The mass of juveniles from the first summer litter of 1996 did not differ significantly between the Control and Exclosure grids ($t_{113} = 0.95$, $p > 0.3$) nor between sexes ($t_{113} = 0.13$, $p > 0.8$) in late July–early August. Later in August, females were heavier in the Exclosure than on Control grids ($t_{27} = 2.5$, $p < 0.02$), but there was no significant difference among grids in the mass of males ($t_{13} = 0.45$, $p > 0.6$). Females weighed on average 50.8 g in the Exclosure, 13.7% above their mean weight on Control grids, 44.7 g. Males weighed on average 43.9 g on all grids combined.

Movements of lemmings

In 1996, both male and female *Dicrostonyx* weighing at least 25 g showed net displacements of less than 1 m d^{-1} , on average, between trap sessions. There were no significant differences among trapping grids (Fig. 7a). In 1997, males showed net displacements of an average of about 5 m d^{-1} between trap sessions, and females

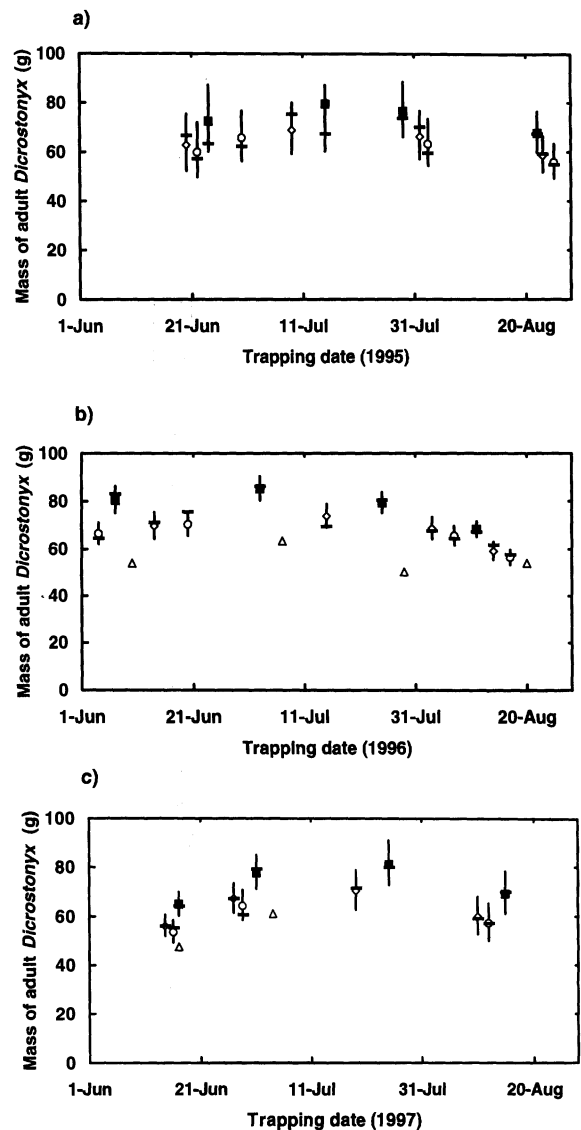


Fig. 6. Mass of adult *Dicrostonyx* caught in (a) 1995, (b) 1996, and (c) 1997 on Control (diamonds and circles) and Exclosure (squares) grids. Points (diamonds, circles, and squares) show the mean body weights of adults (i.e. > 40 g when first captured) estimated with a general linear model. Error bars represent 95% confidence intervals. Horizontal lines show the actual mean weights of adults captured during each time period on each grid. Triangle symbols show the actual mean weights of adults captured on Control grid 3 in 1996 and 1997, which were not included in the model but were plotted to provide additional information about adults on Control grids. Means were calculated based on $\log_{10}$ transformed data.

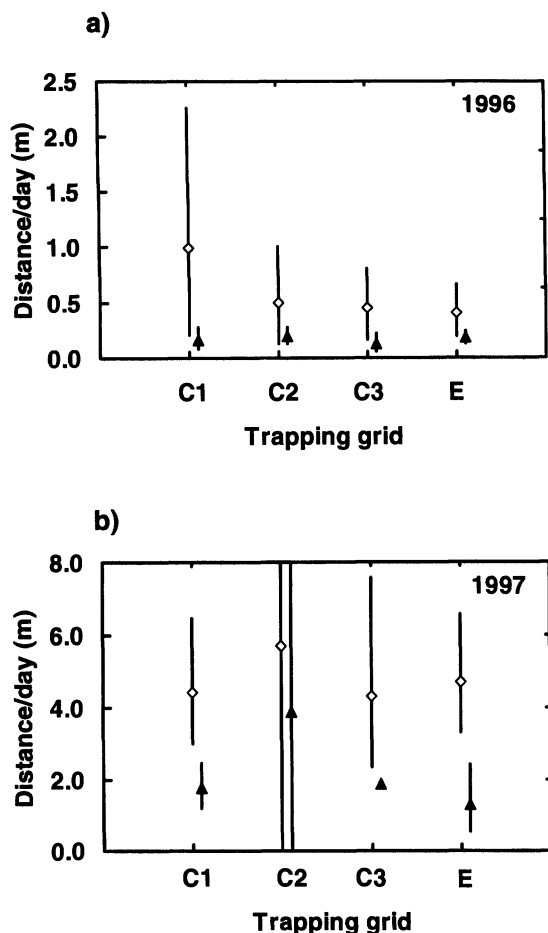


Fig. 7. Means and 95% confidence intervals of net displacement distances between successive primary trapping sessions of large and medium-sized *Dicrostonyx* in 1996 and 1997, on Control (C1, C2, C3) and Exclosure (E) grids. Males are indicated by open diamonds and females by filled triangles. Means were calculated based on $\log_{10}$ transformed data. Note the different scales in (a) and (b).

about 2 m d^{-1} . Again, there were no significant differences among grids (Fig. 7b). The mean net displacements in 1995 were similar to those in 1997, but since sample sizes were small and confidence intervals large they are not shown.

The fence around the Exclosure was permeable to lemmings and we observed runways crossing it. In 1996 and 1997 some telemetered lemmings moved outside the Exclosure, although the fence was a minimum of 25 m from the edge of the trapping grid (Table 4). In 1995 no telemetered animals left the Exclosure even though the fence was not finished until August. The number of Exclosure animals that crossed the fence in 1996 and 1997 was not lower than expected relative to the number of Control animals that moved more than 25 m from the edges of their grids (log-linear analysis of three-dimensional $2 \times 2 \times 2$ contingency table, $\chi^2_2 = 0.18$, $p > 0.9$).

Dispersal and survival of juveniles

In a simultaneous study of juvenile dispersal at this location in 1996, sexually immature *Dicrostonyx* weighing 11–40 g in the Exclosure and on one Control grid were fitted with small glue-on radio transmitters or with radio collars (Blackburn et al. 1999). There was no significant difference between treatments in home range size or mean or maximum distance between fixes, and no juveniles dispersed from the small home ranges (95% c.i. of mean area 69–145 m^2) where they were initially caught. We have a few observations of juvenile movements in other years. In 1995 an 18 g female moved 248 m from where she was initially caught in 9 d and a 20-g male moved 41 m in 5 d. In 1997 a sexually mature 35-g male moved 250 m in 12 d, and a 17-g male tagged at the research camp was trapped 21 d later, 800 m away on Control 2 grid.

The fates of the 14 *Dicrostonyx* with radio collars from the above study are included in our results presented here (Table 4). Of the juveniles with glue-on radios, which fell off and were retrieved within 3–7 d, the fates of 29 from the above study and 14 not previously reported are shown in Table 5. Three individuals (17%) were killed on the Control grid compared with zero in the Exclosure, and 44% were lost from the Control grid compared with 12% from the Exclosure. No non-predation mortalities were recorded. The proportions of animals depredated, lost, and that shed their radios differed significantly between the Exclosure and Control grids ($\chi^2_2 = 12$, $p < 0.005$).

Discussion

In the following discussion we first examine alternative hypotheses to account for the observed increased mass of individuals within the predator exclosure. We next conclude from our experimental and radio-telemetry

Table 5. Fates of immature *Dicrostonyx* fitted with glue-on radios, including 29 individuals reported by Blackburn et al. (1999) and 14 not reported in that study. "Lost" means both the lemming and its radio were never found.

	1996	
	C	E
Animals with glue-on radios	18	25
Radio found off	7	22
Lost	8	3
Mortalities due to predation	3	0
Pomarine jaeger	1	0
Ermine	2	0
Non-predation mortalities	0	0
% depredated	17	0
% non-predation mortalities	0	0
% total mortalities	17	0
% lost	44	12

of *Dicrostonyx* during the peak and decline summers studied, but that the magnitude of the limitation was greater in the decline. Finally, we describe effects of predation on the cyclic dynamics of the lemming population.

Effects of predator reduction on mass

Both male and female adults (animals weighing over 40 g when first caught) were larger within the Exclosure than outside throughout the experiment (Fig. 6). Female juveniles from the first summer litter in 1996 also weighed more, on average, in the Exclosure than on Control grids by the time they reached adult size in August. The size differences could have resulted from increased survival in the protected area, in two ways. First, individuals that survived and had not yet reached their adult weight continued to grow. Second, individuals that had stopped growing remained in the population longer within the Exclosure than outside, and were not replaced during the summer. All the very large adults we caught in June were over-wintered animals, born the previous summer or autumn. Only one spring-born juvenile in 1996 and one in 1997 grew larger than 80 g (both females). Therefore, the very large animals that we continued to catch throughout both years were most likely also over-wintered adults. The survival of these animals was enhanced in the Exclosure relative to that of Control animals both in the previous autumn when they were growing, and after their size stabilised. Larger size of non-cyclic *Microtus agrestis* in some years was also correlated with longer survival (Agrell et al. 1992). An alternative hypothesis is that the larger size was due to better nutrition enabled by changes in foraging behaviour as a result of lowered risk of predation. This phenomenon, known as risk-sensitive foraging (RSF), is discussed further below. These two hypotheses are not mutually exclusive.

It is possible that the larger size of animals in the Exclosure was due to the same causes as the phenomenon first observed by Chitty (1952), in which microtines are heavier in the peak phase of a cycle. The "Chitty effect" has not been explained but a number of alternative hypotheses have been proposed (reviewed by Stenseth and Ims 1993). The relationship between skull size and body size of lemmings also changes during the cycle (Krebs 1964b). The changes could be genotypic (Chitty 1960), perhaps the result of selection for breeding in an increasing population or for aggression in a high-density population (Boonstra and Krebs 1979). In our study, the larger size was evident even in August 1995 and June 1996 when densities were similar among grids and selection pressures should not have been stronger in the Exclosure than elsewhere. The large animals did not appear to have a high reproductive rate, since we found no differences in the proportions

of males or females that were in reproductive condition in the Exclosure compared with Control grids. We conclude that we have no evidence of a difference in reproductive rate between the treatments. These results do not support the hypothesis of genotypic change, but they are insufficient to rule it out. A second hypothesis to explain large size in peak populations is that growth rate varies according to the season (summer or winter) in which the animal develops (Malcolm and Brooks 1993) and age structure shifts as a result of differential reproductive and survival rates among cohorts. Specifically, Malcolm and Brooks (1993) proposed that during the peak there is a high proportion of animals that developed in winter, which are larger than those that develop in summer. Finally, since heavy animals have been observed in high-density non-cyclic populations (Tamarin et al. 1984, Lidicker and Ostfeld 1991) and in non-peak years in cyclic populations (Chitty and Chitty 1962, Krebs 1964a, Lidicker and Ostfeld 1991), it has been argued that they occur simply when conditions favour growth and survival (Lidicker and Ostfeld 1991, Agrell et al. 1992). The mechanisms we postulated in the preceding paragraph, to account for the difference in mass of animals between our experimental treatments, incorporate elements of both the latter hypotheses.

Predation as a limiting factor of *Dicrostonyx* populations

The results of our predator exclosure experiment support the hypothesis that predation was necessary to limit density of *Dicrostonyx* during the summer decline phase of the cycle (1997). All five predictions of this hypothesis were met. First, the great majority of mortalities on Control grids were due proximately to predation. Second, density increased in the protected area relative to Controls. Third, both mark-recapture and Kaplan-Meier estimates of survival within the Exclosure were higher than on Control grids in 1997. Fourth, no other sources of mortality increased enough to negate the effect of reduced predation. Fifth, emigration did not rise nor did reproduction drop to offset the increased survival within the Exclosure.

Support for the hypothesis that predation was necessary to limit the population in the summer of the peak phase (1996) is more ambiguous. Our first, second, and fifth predictions were met. However, in 1996 neither method of estimating adult survival led to consistently higher estimates within the Exclosure, and the proportions of total mortalities of radio-collared animals were about equal between the Control and the Exclosure grids (Table 4). In 1996 mortality was low (Fig. 5b); hence the predation rate was also low. Therefore, experimentally reducing predation could have only a limited effect on survival. Still, although the adult survival rate

was only slightly higher within the Exclosure than on Control grids, it was apparently sufficiently so to lead to greater density in the Exclosure. As well, the considerable reduction in lost glue-on transmitters in the Exclosure suggests that juvenile survival was much improved there compared with Control grids (Table 5) since juveniles did not disperse and the rate of radio failure should not have varied among grids. Therefore, we conclude that our results support the hypothesis that predation was necessary to limit density in the peak summer. However, the magnitude of the limitation was smaller during the peak than during the decline as evidenced by the relative differences in density observed between treatments during the two years (10-fold in 1997 but only two-fold in 1996). Predation may limit the population only while density remains below a level at which some other factor becomes limiting.

If predation were sufficient (as well as necessary) to limit the lemming population in the peak and decline summers, then no manipulation other than predator reduction would cause the density increase we observed in the predator exclosure. We do not have direct evidence about the effects of other factors on density, but the small improvement in survival from reducing predation in the peak suggests that other loss factors might also be limiting then. However, the low survival rate on Controls (Fig. 5c) and the considerable reduction in mortalities in the Exclosure during the decline (Table 4) imply that no other loss factor was significantly limiting in that summer. Production factors and social factors can also limit population growth. During the peak, a smaller proportion of animals was in reproductive condition than in the increase and decline phases (Wilson 1999), implying that food or space may have been limiting. However, in the low-density declining population effects of food and space may have been small relative to the high impact of predation. In summary, these results suggest that predation may have been a sufficient limiting factor during the decline, but probably not during the peak phase.

Up to this point we have not discussed possible impacts of predation upon behaviour and reproduction. If lemmings forage in a risk-sensitive manner (Mangel and Clark 1988, Lima and Dill 1990), the absence of predators might also result in better physical condition of animals and an increased birth rate. In 1996, juvenile *Dicrostonyx* in the Exclosure were found twice in succession in the same burrow less often than were juveniles on a Control grid (Blackburn et al. 1999). One interpretation of this result is that protected juveniles foraged further from shelter and moved among burrows rather than staying close to one refuge. The risk-sensitive foraging (RSF) hypothesis leads to the following predictions within the Exclosure: larger animals, and either a greater proportion of animals in reproductive condition, or larger litter sizes. As dis-

cussed above, we did find larger animals in the protected area, but no difference in the proportion of reproductive individuals; we have no data on litter sizes. In short, we cannot reject the RSF hypothesis; the possibility remains that in our experiment reduced predation risk led to enhanced recruitment, resulting in an increase in density that was confounded with the density increase that resulted from enhanced survival. This potential secondary effect of predation represents an opportunity for further research.

Criticisms of the predator exclosure experiment

Because the predator reduction treatment was not replicated within any year we cannot discount the possibility that the habitat was better there. This problem is common to most large-scale field experiments, in which replication is usually limited. The total area of shrubby habitat on the Exclosure grid did exceed that on the Control grids, although the difference was not statistically significant (Table 1). The area of shrubby habitat is in any case an underestimate of the habitat available to collared lemmings. Although *Dicrostonyx* prefer this habitat type, they were caught in wet meadows, dominated by sedges and grasses, in both 1996 and 1997 at Walker Bay (Morris et al. in press). Sedge-grass habitats accounted for most of the non-shrub habitat on all the grids used in the present study, and were most common on Control grids 1 and 3. Morris et al. (in press) showed that the choice of habitats by *Dicrostonyx* was a function of their own density and that of *Lemmus*. When both species were at low density, *Dicrostonyx* mainly used hummocky (shrubby) habitats and *Lemmus* used wet meadows. When both species were at high density, both used both habitats. However, the density of *Dicrostonyx* in their preferred habitat was reduced relative to what it otherwise would have been as the density of *Lemmus* increased in the same habitat.

Each hectare of dry land in the Exclosure represented on average about 22% more shrubby habitat than did a hectare on Control grids. In contrast, we observed very large differences in *Dicrostonyx* density between the treatments: in the predator exclosure density rose to double that on Controls in 1996, and 10 times that in 1997; these differences were detectable by *t*-tests with only 2 and 1 degrees of freedom. If density is calculated per ha of shrubby habitat, instead of per ha of dry land, the differences between the treatments in August of each year remain significant (one-tailed *t*-tests; 1996: $t_2 = 2.6$, $p < 0.061$; 1997: $t_1 = 10.2$, $p < 0.035$). Finally, if habitat were substantially superior within the Exclosure, density there should have exceeded that on Control grids before the protective structure was complete and each spring when the structure was likely just beginning to be effective. Instead, density within the Exclosure was similar to that on Control grids in 1995

and early in the summer of 1996, and to that on Control 1 grid early in 1997 (Fig. 2). The subsequent density increases in the Exclosure relative to Controls occurred in the apparent absence of differences in reproductive rates or lemming movements. We conclude that most of the observed differences in density resulted from the experimental treatment.

The increased density in 1996 without a significant increase in survival in the protected area makes it worth considering whether secondary experimental effects other than predator reduction could have enhanced the density of lemmings in the Exclosure. A second factor that could have increased density within the Exclosure is restricted emigration due to a partial fence effect (Krebs et al. 1969). However, neither the net distances moved by lemmings nor the proportions of lemmings that travelled away from their grids differed significantly between treatments. The most parsimonious explanation for the observed density increase is that it was due to the experimental treatment of reduced predation.

Predation within the Exclosure may have been intensified late in the season because predators were attracted to the abundant prey within. Ermine and foxes appeared in the Exclosure in mid-August of both 1996 and 1997 and snowy owls perched on the posts that supported the overhead mesh in September 1996. The high survival estimate from mark-recapture data in August 1997 includes only up to 16 August, but survival may have subsequently declined in the autumn of both years. The attraction of predators to local hotspots of high prey density, termed a "pantry effect" (Batzli 1985), has plagued other food-addition and predator-removal experiments. Reid et al. (1995) found that their predator exclosure did not enhance recruitment because juvenile lemmings in a low-density population dispersed outside and were not replaced by reciprocal immigration. We observed no juvenile dispersal in 1996 (Blackburn et al. 1999) but our few observations from 1995 and 1997 suggest higher rates of juvenile dispersal in years of lower density. Dispersal of juveniles may therefore have diluted the effect of predator removal in the decline phase.

Changes in predation rate during the cycle

In the decline summer of our study, the survival rate was lower than in the peak summer (Fig. 5b, c) and a larger proportion of animals died as a result of predation (Table 4). A low predation rate at very high prey density is predicted when the functional and numerical responses of predators are asymptotic (Holling 1959). Further, a delayed numerical response of predators can elevate the predation rate at declining prey density, known as delayed density-dependent predation. Increases in ermine numbers commonly follow microtine

peaks (Maher 1967, MacLean et al. 1974, Fuller et al. 1975a, Fitzgerald 1977, Korpi-mäki et al. 1991, Korpi-mäki 1993, Sittler 1995). In our study ermine were most abundant in 1996 and 1997 and were responsible for most known predation events in 1997 but few in other years. Arctic foxes were most abundant in 1996 and did not seem to be more numerous in the decline summer than in summers preceding the peak (Wilson 1999). The survival rate of radio-collared animals on Control plots tended to decrease as the population declined in the summer of 1997 (Results and Fig. 5c). During the same period, the difference in density between the Exclosure and Control grids increased (Fig. 2). These trends imply an inversely density-dependent (depensatory) predation rate during the summer of the decline phase. Again, this pattern is expected to occur unless predator numbers fall sharply or functional responses follow a sigmoid (Type III) curve within the relevant range of prey densities (Holling 1959).

Implications for lemming population dynamics

The lemming population decline began in autumn 1996 or winter 1996–1997, when we were not present, and when the predator exclosure was less effective than in summer. Hence our results cannot show whether predation initiated the decline, which then continued into the following summer (1997). The only lemming predators present in winter are arctic foxes, snowy owls, and ermine. Ermine are adapted to hunt under the snow (Fitzgerald 1977), and high rates of occupation (up to 14%) by ermine of lemming nests in Greenland implied that they killed a large proportion of the lemming population in winters when it was declining (Sittler 1995). At Pearce Point, N.W.T., where the lemming population was non-cyclic, up to 7.6% of lemming and vole nests were occupied by ermine (Reid and Krebs 1996). However, the intensity of ermine predation was not significantly related to the population growth of microtines in two winters, and Reid and Krebs (1996) hypothesised that the ability of ermine to limit the lemming population in winter might depend on temperature and snow depth. It is not known to what extent the ability of arctic foxes and snowy owls to hunt lemmings is restricted by snow cover.

Four effects of predation on the population cycle of *Dicrostonyx* are evident from our results. First, predation depresses the peak density. Second, predation reduces densities during the decline phase, leading to a depressed minimum summer density. These two effects follow from our demonstration that predation limited the lemming population in the summers of both the peak and decline phases of the cycle. During the peak, the proportion of telemetered animals that died was similar inside and outside the experimental predator

enclosure; hence other mortality factors might depress peak density in the absence of predation. Third, predation may reduce population density throughout the summer increase phase, since the same proportion of animals was depredated on Control grids in 1995 (the increase phase) as in 1996 (the peak). Fourth, in unprotected populations predation may extend the duration of the decline, further lowering minimum density, since when numbers were still declining on Control grids in July and August 1997, density began to increase within the predator enclosure (Fig. 2); that is, the decline was reversed within our experimental treatment. This result implies that predation was the primary cause of declining densities in summer. In another paper (Wilson unpubl.), estimates of the winter abundance and diets of predators, and indicators of reproduction in lemmings, are analysed to test the hypothesis that predation was a necessary cause of the lemming population decline that began in autumn or winter.

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