

**EFFECTS OF PREDATION ON THE POPULATION DYNAMICS OF LEMMINGS
AND ON LOSS OF GOOSE NESTS**

by

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ABSTRACT

Collared lemmings (*Dicrostonyx groenlandicus*) fluctuate periodically in abundance on the Kent Peninsula, Northwest Territories, Canada. I tested whether predation was necessary to (1) limit the lemming population during a peak and decline summer (1996 and 1997), and (2) cause the population decline. The nesting success of geese also fluctuates at this location. I tested whether the relative number of goose nests lost could be predicted from functional and numerical responses of nest predators to lemming density.

I reduced predation on lemmings with a fence and an overhead mesh of monofilament line over 11 ha, completed during the lemming increase (summer 1995). I used mark-recapture and radio-telemetry to investigate demography in this "Exclosure" and three Control areas, and estimated winter predation from droppings and abundance of predators.

Density increased in Exclosure relative to Controls in both summers. Survival was significantly higher within Exclosure during the lemming decline only. Neither proportions of reproductive animals nor net movements differed significantly between treatments. I conclude that predation was a necessary limiting factor in the peak and decline summers, but that the magnitude of limitation was greater in the decline.

Density declined over winter on all sites. The next summer (1997), the decline accelerated on controls but was reversed within Exclosure. Summer survival was lower in the decline than in the peak. Lemmings stopped reproducing early in the peak summer. If there was no winter breeding, winter survival was high. The contribution of predation to the winter decline depends on the extent to which mortality factors were compensatory. I conclude that predation may not have been necessary to cause the decline; instead the decline was initiated by cessation of reproduction. However, predation accelerated and extended the decline the next summer.

From observed responses of nest predators to lemming density, I predicted that the number of goose nests depredated should be lowest during lemming peaks. This was not true in past lemming cycles in this region (1989 – 1994). I conclude that nest loss cannot be predicted from the phase of the lemming cycle alone, and make testable predictions of how other factors should affect nest loss.

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PREFACE

Chapters 2 and 4 of this thesis have been submitted for publication as follows:

Chapter 2:

Wilson, D.J., Krebs, C.J., and Sinclair, A.R.E.. Limitation of collared lemming populations during a population cycle. *Oikos*, accepted February 12, 1999.

I conducted the field research for this paper, analysed the data, and wrote the manuscript. My co-authors acted as advisors.

Chapter 4:

Wilson, D.J. and Bromley, R.G. Functional and numerical responses of predators to cyclic lemming abundance: effects on loss of goose nests. *Oikos*, submitted September 2, 1998.

The manuscript was not accepted, but we were invited to submit a revised version and we will do so in 1999.

Dr. Bromley acted as my advisor for the part of my research reported in this paper. He first noticed a possible link between goose nesting success and lemming abundance on the Kent Peninsula. The paper incorporates his long-term data of nesting success (1987 – 1997) and annual surveys of relative lemming abundance (1990 – 1997), as well as a helicopter survey of territorial pairs of pomarine jaegers in 1996 and several observations of the behaviour of geese and predators. I designed and conducted field research (1995 – 1997) to quantify the relative abundance and behaviour of predators and their interest in artificial goose eggs. I analysed the data and wrote the paper, with advice from Dr. Bromley.

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The most discouraging part of this project was analysing predator scats and pellets, and I never could have done it without the help of many painstaking people. I am particularly grateful

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Without the encouragement and good cheer of my wonderful friends and family, I would have finished this project in much worse condition. Thank-you Christine Adkins, Lance Barrett-Lennard, Frances Cassirer, Patricia Colosimo, Steve Cumming, Dave Forsyth, Kathy Heise, Rachel Holt, Leah MacFadyen, James McCormick, Gail Sandercock, Detmar Schwichtenberg, Diane Srivastava, Harald Steen, Jenny and James Wilson, all my friends in the East, and most specially, Mum and Dad.

CHAPTER ONE

INTRODUCTION

Lemmings fluctuate periodically in abundance throughout most of the Arctic. The causes of this intriguing phenomenon have been sought for 75 years since it was first recognised by Elton (1924). Understanding was initially slow because the results of observational and correlational studies, of both lemmings and related species, were perplexingly inconsistent. More recent experimental studies of small mammal ecology, most on vole populations, have led to faster advances (Stenseth and Ims 1993a). As well, the technology of radio-telemetry has made it possible to study the movements and survival of individuals. Still, few experiments have been conducted on wild populations of lemmings because in the far north such research is costly and arduous.

Lemmings are small rodents broadly distributed through the Holarctic. Known as microtines, in the family Muridae and subfamily Arvicolinae (formerly Microtinae), lemmings' closest relatives are voles and muskrats. Two genera of lemmings are almost circumpolar – collared lemmings (*Dicrostonyx*) in arctic North America, Greenland, and Siberia, and brown and Norwegian lemmings (*Lemmus*) in Siberia, all but the eastern regions of northern North America, and Fennoscandia (Jarrell and Fredga 1993). Although the two are often sympatric, *Lemmus* is generally found in moist tundra habitat dominated by grasses and sedges, and *Dicrostonyx* often on drier tundra dominated by shrubs (Fuller *et al.* 1975a, Rodgers and Lewis 1986a, b).

Characteristics of lemming cycles

Patterns of lemming cycles have been reviewed by Krebs and Myers (1974) and more recently by Krebs (1993) and Stenseth and Ims (1993b), and several long-term data sets have been published (e.g. Pitelka 1973; Fuller *et al.* 1977; Framstad *et al.* 1993a, 1993b). Lemming cycles typically have a period of 3 to 4 years and amplitudes between 25:1 and 200:1 (Krebs 1993). Cycles are often synchronous over large geographic areas and among sympatric species. Growth to the peak density is explosive, usually within one year. A rapid decline follows; it is often more variable in rate than the increase, and may occur in any season and last one or more years. The low phase is usually the longest and may last more than two years.

Although the data are sparse, several characteristics of lemmings and their environment seem to vary consistently within a cycle. During the peak phase, body size may be greater than at other times (Krebs 1964a). The maturation rate and length of the breeding season are lowest at the peak, but pregnancy rates and litter sizes are relatively invariant through the cycle (Krebs and Myers 1974). Winter reproduction is thought to be common in the year before the peak but uncommon at other times (Kaikusalo and Tast 1984). The rate of winter mortality seems to be low, except during certain declines (Krebs 1993). Damage to vegetation is sometimes, but not always, evident during or after a peak phase (Krebs and Myers 1974). It is well known that predators increase in numbers during lemming peaks; their per capita consumption of lemmings also increases when these prey are abundant (Reid *et al.* 1995, and see Batzli *et al.* 1980).

Hypotheses for the causes of lemming cycles

Many hypotheses have been advanced to explain rodent population cycles: Batzli (1992) listed twenty-two. The rapid increase phase of microtine cycles is not surprising given the fecundity of these animals. Most research has focussed on causes of the decline. Hypothetical mechanisms causing cycles are traditionally separated into intrinsic and extrinsic factors; both

types are proposed to result in cycles owing to delayed density dependence. In the following paragraphs I summarise the major categories of hypotheses.

Intrinsic hypotheses emphasise the importance of differences among individuals. Proportions of individuals of different genotypes or phenotypes may vary during the cycle as a result of differential selection, maternal effects, or social interactions (Chitty 1952, 1996; Krebs 1978, 1996). Demographics may vary not only in response to changing density, but as a result of fluctuation in the composition of the population. There is a growing body of work on the social structure of voles, but apart from a few studies of aggression (Semb-Johansson *et al.* 1979, Heske and Jensen 1993, Heske *et al.* 1993), home range, and dispersal (Brooks 1993, Reid *et al.* 1995, Blackburn *et al.* in press), little is known about this aspect of lemming behaviour (Krebs 1993, 1996).

Fluctuations in extrinsic factors – disease, food quantity or quality (nutrients and secondary plant compounds), and predation – could hypothetically cause microtine cycles. Few studies have been able to associate population cycles with pathogens, although levels of virus were higher in voles (*M. pennsylvanicus*) in a declining population (Desicoteaux and Mihok 1986). Little is known about lemming pathogens or their population effects. Although supplemental feeding of voles affects reproduction, growth, and survival, the addition of food has never prevented a decline (Stenseth and Ims 1993b) unless predators were excluded (Ford and Pitelka 1984). However, because voles (*Microtus agrestis*) showed poor growth and reproduction when introduced into habitats that had previously supported high vole densities, Agrell *et al.* (1995) suggested that food quality might have been impacted by the abundant voles in the previous year.

Most experimental removals of vole predators have been on a small scale and resulted in increased densities but did not affect population dynamics (Erlinge 1987, Desy and Batzli 1989). More recently, the exclusion of predators from an 11.2 ha area prevented seasonal declines in a

non-cyclic population of collared lemmings, and resulted in enhanced recruitment and adult survival (Reid *et al.* 1995). When Norrdahl and Korpimäki (1995b) removed either avian predators or least weasels from large areas, the density of voles did not increase, but when they removed avian predators, least weasels, and ermine, vole densities increased within the removal areas while they continued to decline elsewhere (Korpimäki and Norrdahl 1998). It has also been recognised that predation may interact with prey behaviour to affect factors other than mortality – growth and reproduction may be impacted if animals alter their foraging patterns in response to a high risk of predation (Lima and Dill 1989, Korpimäki and Krebs 1996).

The consistent cyclic changes that have been observed in reproduction, body size, and the abundance of predators suggest that multiple factors interact to generate microtine cycles (Batzli 1992). There is a growing consensus that predation and intrinsic factors may both be necessary to generate declines (e.g. Krebs 1996, Stenseth *et al.* 1996).

Indirect effects of lemming abundance on other prey species

The swings in predator numbers and diets in response to changing lemming density affect other prey species. Roselaar (1979) suggested that the numbers of migrating shorebirds would fluctuate if predators ate their eggs and young in years when lemming numbers were low. Summers (1986) later associated regular fluctuations in the abundance of young brent geese (*Branta bernicla*) in Britain with published observations of lemming abundance on the Taymyr Peninsula in Siberia, where the geese breed. More rapid reproduction by predators during lemming peaks might lead to particularly severe loss of goose nests the following year (Dhondt 1987, Summers and Underhill 1987). Until lately, field research to test these hypotheses has been absent or short-term, and the reality of the relationships has been controversial. Recently, in a 6-year study on the western Taymyr, Spaans *et al.* (1998) found that the system was not as simple as had been supposed. They observed a delayed numerical response of arctic foxes after

one lemming peak, but not after another, when even though no nests were taken, most goslings were killed by gulls.

Lemmings and geese on the Kent Peninsula, N.W.T.

Populations of collared lemmings (*Dicrostonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) have peaked every three years since 1984 on the Kent Peninsula, N.W.T., Canada (Poole and Boag 1988, Cotter 1991, Chapter 4). The rates of nest success of white-fronted geese (*Anser albifrons*) and Canada geese (*Branta canadensis*) on the Kent Peninsula have fluctuated widely since 1987 (Bromley *et al.* 1995). Nesting success was synchronous between the two species of geese and most nest failures were due to predation by arctic foxes and avian predators.

Thesis questions

The research reported in this thesis focussed on two main questions: (1) How does predation affect the population dynamics of lemmings, and (2) How do fluctuations in lemming abundance affect the loss of goose nests? I used a combination of experiments and observations to study collared lemmings and their predators during four summers on the Kent Peninsula. To test experimentally the population effects of predation, I built a predator enclosure consisting of a fence and an overhead mesh of monofilament, over 11 ha of tundra. The structure was completed late in summer 1995, a lemming increase year. I live-trapped lemmings to estimate their abundance and reproductive condition (Tables 1-1, 1-2), and estimated their survival with radio-telemetry in the summers of 1994 – 1997. I monitored the reproductive success of predators and estimated their summer and winter diets from pellets and scats. Finally, I built simple simulation models to test whether the estimated demographic parameters could cause the observed population decline (1996 – 1997).

To test for possible indirect interactions between lemming abundance and the loss of goose nests, I assessed numerical and functional responses of nest predators to lemming density. I recorded sightings of predators and observed them foraging in prime goose nesting areas. I supplemented nest predation data collected by the N.W.T. government (Bromley *et al.* 1995) by recording attacks on artificial plaster goose eggs, as an index of the total response of predators to lemming abundance.

The structure of this thesis is as follows:

Chapter 1. Introduction.

In this chapter I review the background leading to the questions asked in this thesis, and list the main hypotheses tested.

Chapter 2. Limitation of collared lemming populations during a population cycle.

This chapter describes tests of the hypothesis that predation is necessary to limit lemming populations during the peak and decline phases of the cycle. I report comparisons of density and demography between a population of collared lemmings that was experimentally protected from predation, and three control populations.

Chapter 3. Predation and the decline of collared lemming populations.

In this chapter I describe tests of the hypothesis that predation is a necessary cause of the decline of lemming populations. I compared rates of survival between the peak (1996) and decline (1997) summers, examined evidence of winter predation (1996 – 1997), and compared rates of decline between the protected and control populations. In addition, I compared reproductive parameters among years and used simple population models to test whether the estimated demographic rates could cause the observed decline in winter and summer.

Chapter 4. Functional and numerical responses of predators to cyclic lemming abundance: effects on loss of goose nests.

This chapter describes a test of the hypothesis that the pattern of predation on goose nests (nests lost per km²) during a three-year lemming cycle can be predicted from (1) functional responses of nest predators to lemming density, and (2) timing of numerical responses. I compared the relative abundance of predators on goose eggs and indices of their functional and total responses among three years of the lemming cycle. The pattern of nest losses during a cycle predicted from these results is then compared with data from previous lemming cycles at this location.

Chapter 5. Conclusion.

This chapter summarises the main results reported in this thesis and recommendations for further research.

Table 1-1. Trapping dates in 1994, 1995, 1996, and 1997. Trapping sessions used for MARK analyses in 1996 and 1997 are noted (e.g. Session 1, 96; see Chapter 2).

	Grid	1994	1995	1996	1997
Trap cleaning					
	Control 1	May 30	June 10-11	May 30, June 3	June 13-14
	Control 2	May 30	June 8-9	May 31, June 4	June 13
	Control 3	May 30	June 14	June 2	June 14
	Exclosure	--	June 13	June 1	June 13
Trapping					
					(Session 1, 97)
	Control 1	June 8	June 20	June 14	June 15-16
	Control 2	June 8	June 22	June 20	June 15-16
	Control 3	June 8	June 23	June 10	June 17-18
	Exclosure	—	June 24	June 7	June 17-18
	Control 1	June 29	June 28		
	Control 2	June 28	June 30		
	Control 3	June 29	—		
	Exclosure	—	July 1		
				(Session 1, 96)	(Session 2, 97)
	Control 1	July 9	July 9	July 15-16	June 28-29
	Control 2	July 9	—	July 20-21	June 28-29
	Control 3	July 11	—	July 7-8	July 4-5
	Exclosure	—	July 15	July 3-4	July 1-2
				(Session 2, 96)	(Session 3, 97)
	Control 1	July 23	August 2	August 3-4	July 19-20
	Control 2	July 22	August 2	August 7-8	July 23-24
	Control 3	—	—	July 29-30	—
	Exclosure	—	July 29	July 25-26	July 25-26
				(Session 3, 96)	(Session 4, 97)
	Control 1	August 11	August 23	August 14-15	August 10-11
	Control 2	August 11	August 25	August 17-18	August 12-13
	Control 3	August 13	—	August 20-21	—
	Exclosure	—	August 22	August 11-12	August 15-16
	Control 1	September 1			
	Control 2	August 30			
	Control 3	August 30			
	Exclosure	—		August 24-25	

Table 1-2. Trapping sessions used in analyses of reproductive and age structure data (Chapters 2 and 3). Each season was divided into four periods, as similar as possible among years. Trapping sessions on Control 3 grid were excluded from the analyses requiring comparisons among years.

Period	Grid	1995	1996	1997
June	Control 1	June 20	June 14	June 15-16
	Control 2	June 22	June 4	June 15-16
	Control 3	June 23	June 10	June 17-18
	Exclosure	June 24	June 7	June 17-18
Late June – mid July	Control 1	July 9	July 15-16	June 28-29
	Control 2	June 30	June 20	June 28-29
	Control 3	—	July 7-8	July 4-5
	Exclosure	July 15	July 3-4	July 1-2
Late July – early August	Control 1	August 2	August 3-4	July 19-20
	Control 2	August 2	August 7-8	July 23-24
	Control 3	—	July 29-30	—
	Exclosure	July 29	July 25-26	July 25-26
August	Control 1	August 23	August 14-15	August 10-11
	Control 2	August 25	August 17-18	August 12-13
	Control 3	—	August 20-21	—
	Exclosure	August 22	August 11-12	August 15-16

CHAPTER TWO

LIMITATION OF COLLARED LEMMING POPULATIONS DURING A POPULATION CYCLE

INTRODUCTION

Populations of collared lemmings (*Dicrostonyx* spp.) exhibit multi-annual fluctuations in many circumpolar regions. This pattern has been documented for *D. torquatus* on the Taymyr 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 1986b), 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, Chapter 4), 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 *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 1993b), 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. Marcström *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 (short-tailed weasels or stoats) (*Mustela erminea*), arctic ground squirrels (*Spermophilus parryi*), parasitic, pomarine, and long-tailed jaegers (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 x 300 m (9 ha), in predominantly hummocky habitat (Fig. 2-1). The sites were at least 0.5 km apart and largely separated by

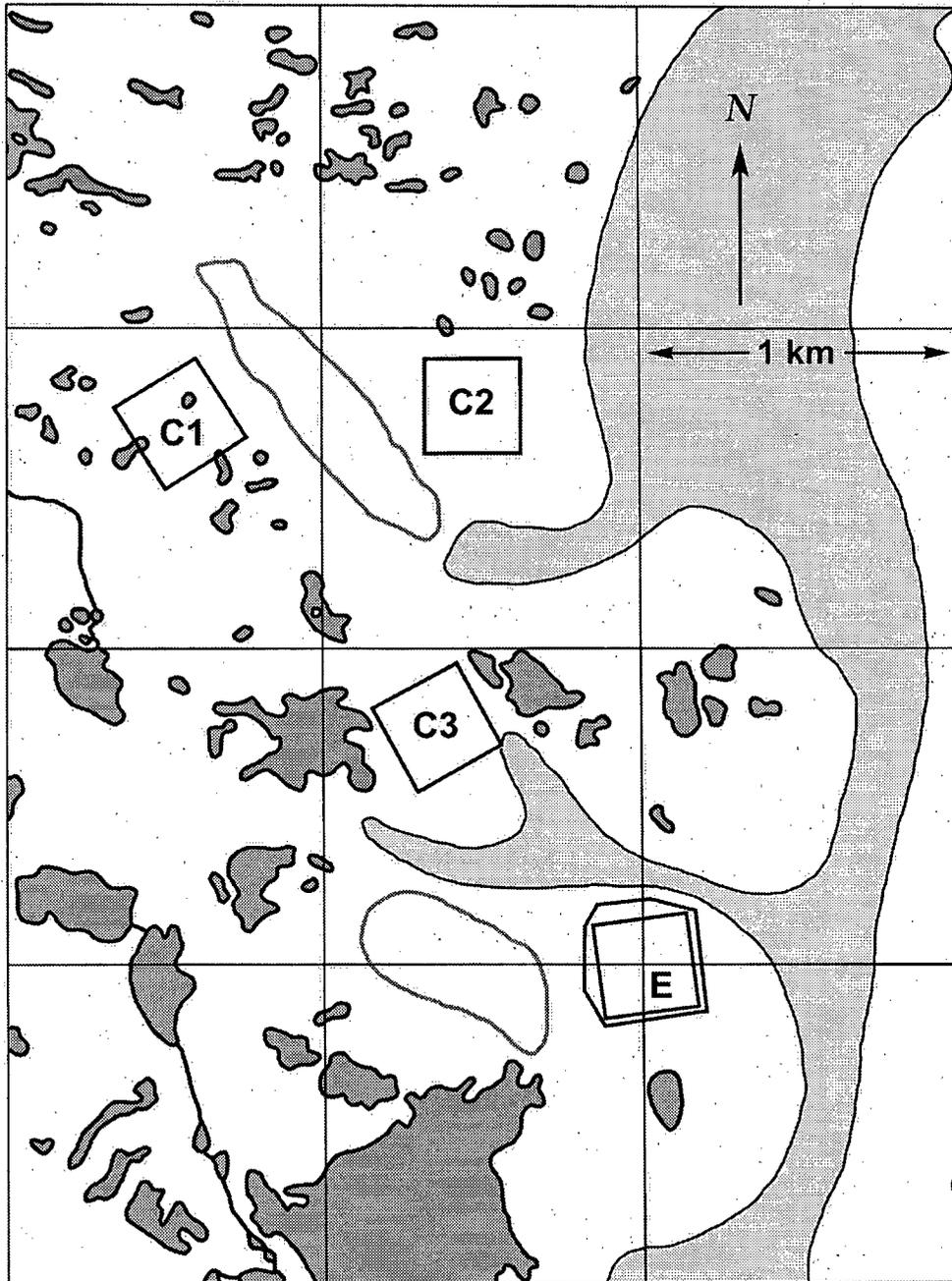


Fig. 2-1. Map of trapping grids at the Walker Bay field station, Kent Peninsula, N.W.T. used in 1994 through 1997. Control grids are indicated as C1, C2, and C3; the predator enclosure is labelled E and the surrounding fence is shown. Dark shading represents the largest lakes and ponds; light shading shows the approximate extent of mud flats. Unshaded contours represent ridges of high ground (< 20 m above sea level).

ridges, ponds, or mud flats. We protected one plot from predators by building a predator enclosure (approximately 11 ha) consisting 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 in July 1995 when it was under construction. 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. We estimate that the risk of predation was reduced by about 50% within the protective structure. 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 on each grid in one-day sessions (trapping in the Enclosure began in 1995; Table 1-1). In 1996 and 1997 we trapped in two-day sessions whenever possible (Table 1-1); 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 Exclosure.

Estimation of density and survival

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

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 2-1). 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 2-1). 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

Table 2-1. 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 : | $c = p_2 = p_1(t) N(t * g) S(t * g)$ |
| | | $c = p_2 = p_1(.) N(t * g) S(t * g)$ |
| (6) | Remove $t * g$ interaction from S : | $c = p_2 = p_1(.) N(t * g) S(t + g)$ |

(1997 model only)

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
.	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; 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.

χ^2_d distribution where the degrees of freedom, d , is 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 used the adjusted t-test for comparing a single observation to the mean of a sample (Sokal and Rohlf 1995, p. 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 days; Control 2: 13, 25, 20 days; Exclosure 14, 24, 21 days). 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 ($S(t + Excl)$), (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-day 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 the study 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, p. 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 (< 25g), medium (25 – 49g), and large (\geq 50g). 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 (Table 1-2). 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, p. 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 an approximation of Akaike's information criterion (AIC) (Akaike 1974). Planned Helmert contrasts (Statistical Sciences 1995, p. 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 (August 24-25).

Sex ratio and age structure

We compared the proportion of male lemmings, and the proportion of lemmings classified as adults when first captured, 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 (Chapter 4). We display estimates of 0.11 ha^{-1} (1 animal per grid) throughout 1994 (Fig. 2-2); 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. 2-2) although 95% confidence intervals were large. Because the predator enclosure was not 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 ($\Delta\text{AIC}_c \leq -1.4$) 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 2-2, 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 ($\Delta\text{AIC}_c = -3.2$, Table 2-2, 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 ($\Delta\text{AIC}_c = -1.8$).

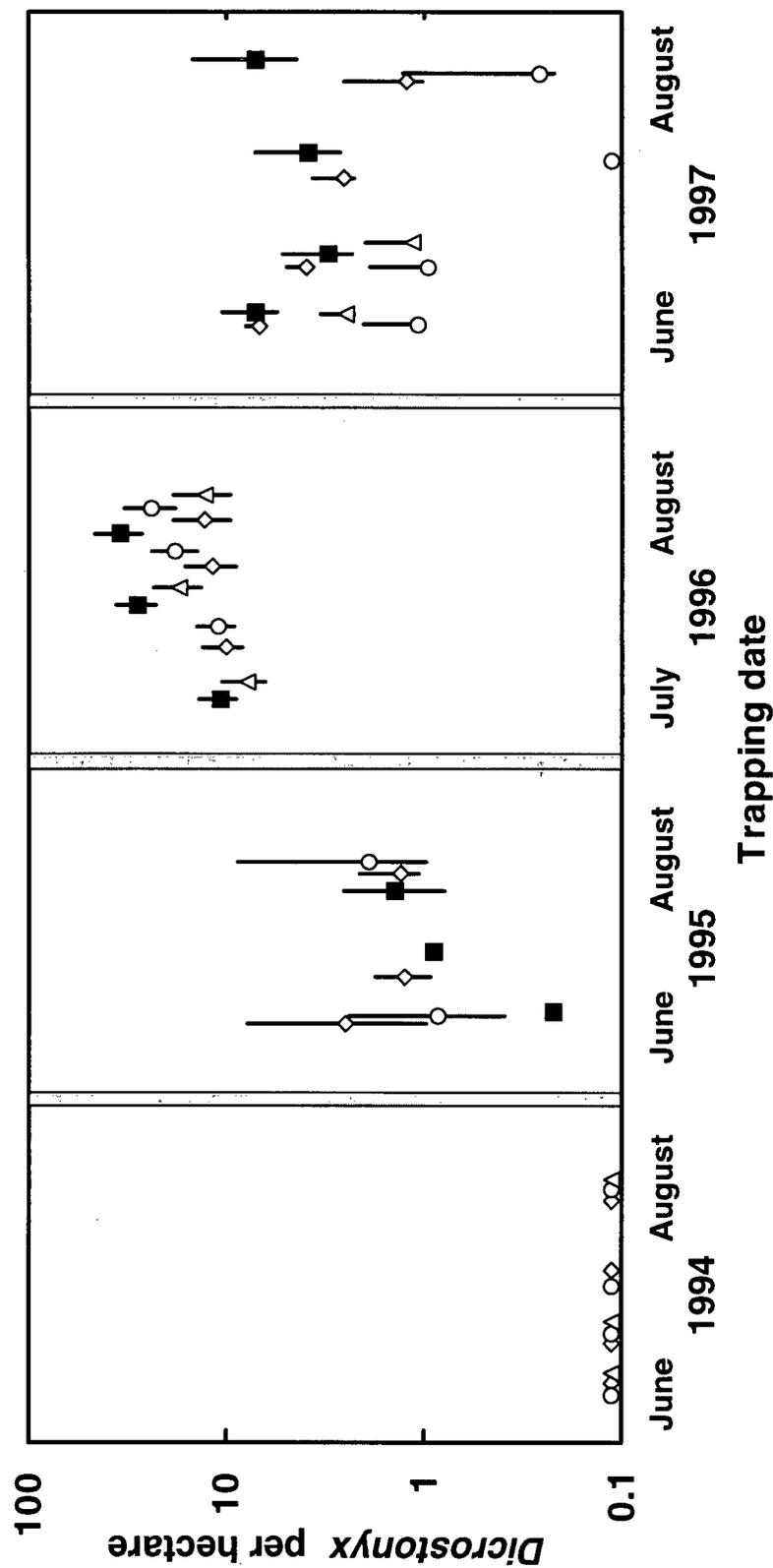


Fig. 2-2. Estimates and 95% confidence intervals of the population densities of *Dicrostonyx groenlandicus* on Control (diamonds, circles and triangles) and Exclosure (squares) grids, in 1994, 1995, 1996, and 1997. Density was estimated in 1995 by means of the Jolly-Seber method and in 1996 and 1997 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. Points without error bars are those for which confidence intervals could not be estimated because of small sample sizes.

Table 2-2. 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 2-1.

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. $c = p_2 = p_1(.)$ N(t * g) S(t * g)	7.8	21

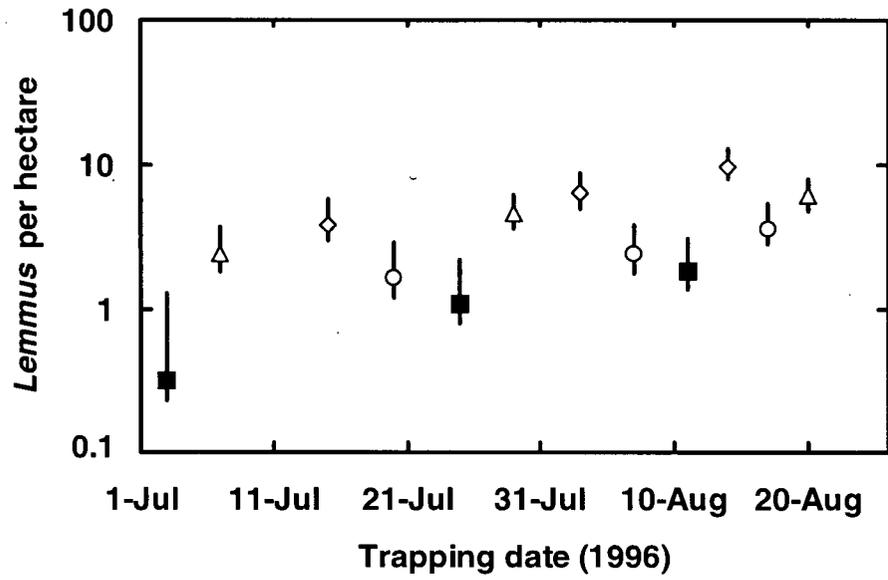
In early July 1996 the estimated density of *Dicrostonyx* was $8 - 11 \text{ ha}^{-1}$ on all grids (Fig. 2-2). In late July the estimated density in the Exclosure was nearly double the mean of the estimated densities on the Control grids (one-tailed t-test, $t_2 = 3.2$, $p < 0.05$). By mid-August the estimated density in the Exclosure was 34.1 ha^{-1} (95% c.i. $26.5 - 46.2$), 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 $1 - 2 \text{ ha}^{-1}$ on two Control grids and 7 ha^{-1} on Control 1 grid and within the Exclosure (Fig. 2-2). 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 $1.0 - 2.5$). Within the Exclosure, the density declined to about 3 ha^{-1} (95% c.i. $2.3 - 5.2$) by 1 July, but by August it rose to approximately 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.

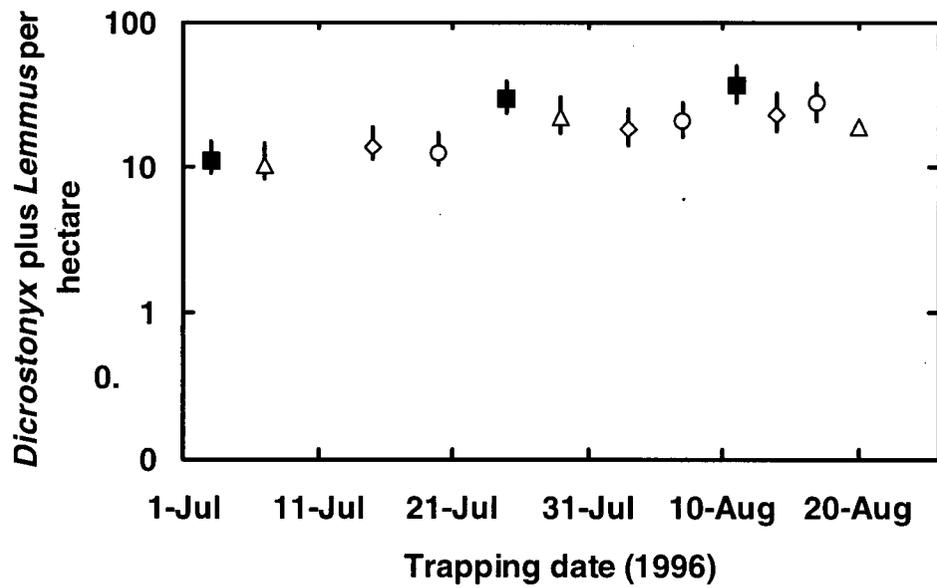
We caught few *Lemmus* except in 1996; in that year we caught few until July but they then increased in abundance on all grids. In 1996 there tended to be fewer *Lemmus* in the Exclosure than on the other grids (Fig. 2-3a); indeed there seemed to be an inverse relationship between the densities of the 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 not significantly different (Figs. 2-2, 2-3a). Because the grids were not chosen to include *Lemmus* habitat, it may be inappropriate to estimate total lemming density. We were not able to do so formally in any case because we could not assume probabilities of capture were equal in

Fig. 2-3. (a) Estimates and 95% confidence intervals of the population density of *Lemmus trimucronatus* on Control (diamonds, circles and triangles) and Exclosure (squares) grids, in 1996, obtained by means of the robust design. (b) Estimates of densities of both species of lemmings on the four grids, obtained by summing data from corresponding trapping sessions in Figs. 2-2 and 2-3a.

a)



b)



the two species ($\Delta AIC_c = 4.2$). Nonetheless, because the question of how total lemming abundance differed among the grids was interesting, we summed the estimated densities of the two species (Fig. 2-3b). The estimated density of all lemmings in the Exclosure in 1996 exceeded the mean of the estimates for 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-day survival rate of *Dicrostonyx* estimated from mark-recapture data was 50% higher in the Exclosure than the mean of the estimates on Control grids (Fig. 2-4). 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. 2-4). 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 + 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 + 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

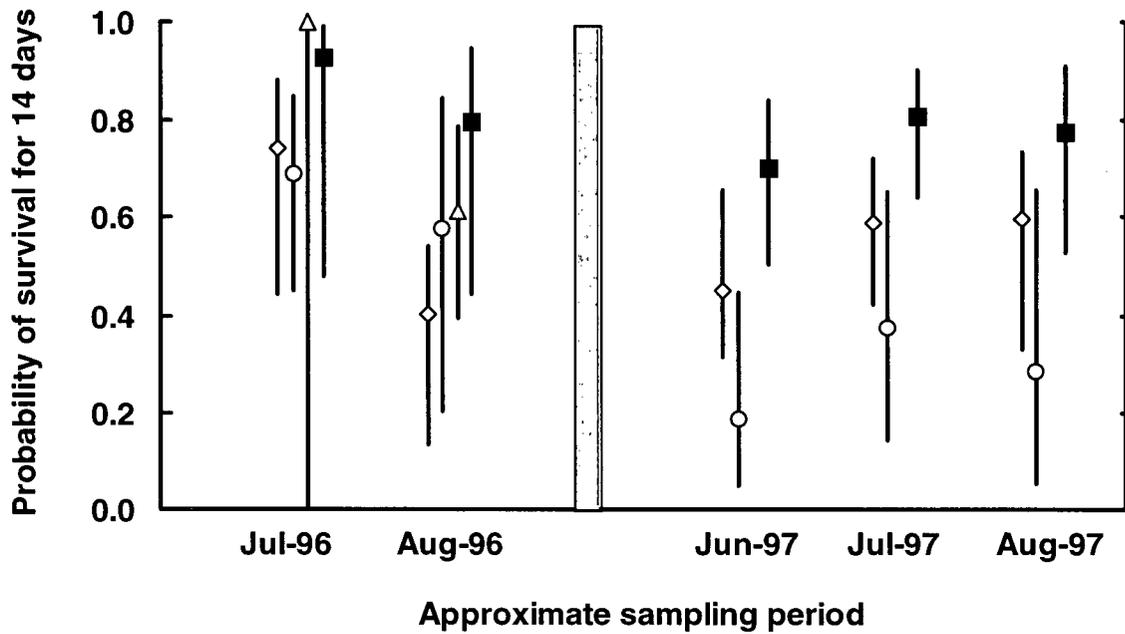


Fig. 2-4. Estimates and 95% confidence intervals from the robust design of the survival of *Dicrostonyx groenlandicus* on Control (diamonds, circles and triangles) and Exclosure (squares) grids, in 1996 and 1997. Survival was measured between the primary trapping sessions for which density estimates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

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 (Fig. 2-5).

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 2-3). The lemmings were killed by arctic foxes in all three years, by ermine in 1995 and 1997, and by various avian predators (Table 2-3). 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 (Chapter 4). 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 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 were 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 2-3).

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 2-3). 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

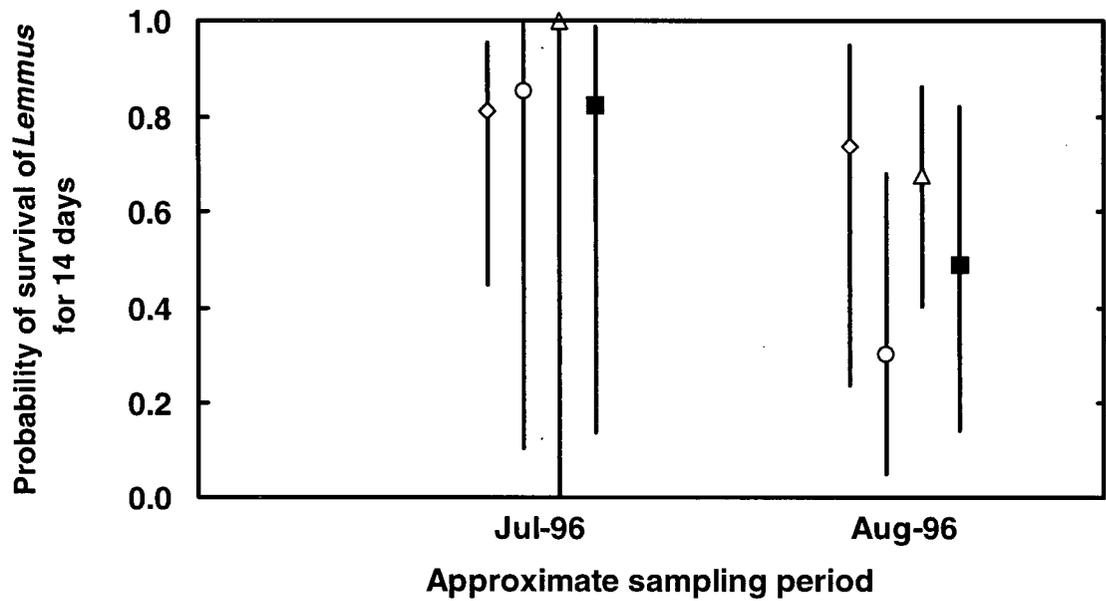


Fig. 2-5. Estimates and 95% confidence intervals from the robust design of the survival of *Lemmus trimucronatus* on Control (diamonds, circles and triangles) and Exclosure (squares) grids, in 1996. Survival was measured between the primary trapping sessions for which density estimates are plotted in Fig. 2-3.

Table 2-3. 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 1 animal in 1995 and 3 in 1996 that died within 2 days of being radio-collared.

	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

^a all in August

^b 4 on 28 June and 1 on 17 August

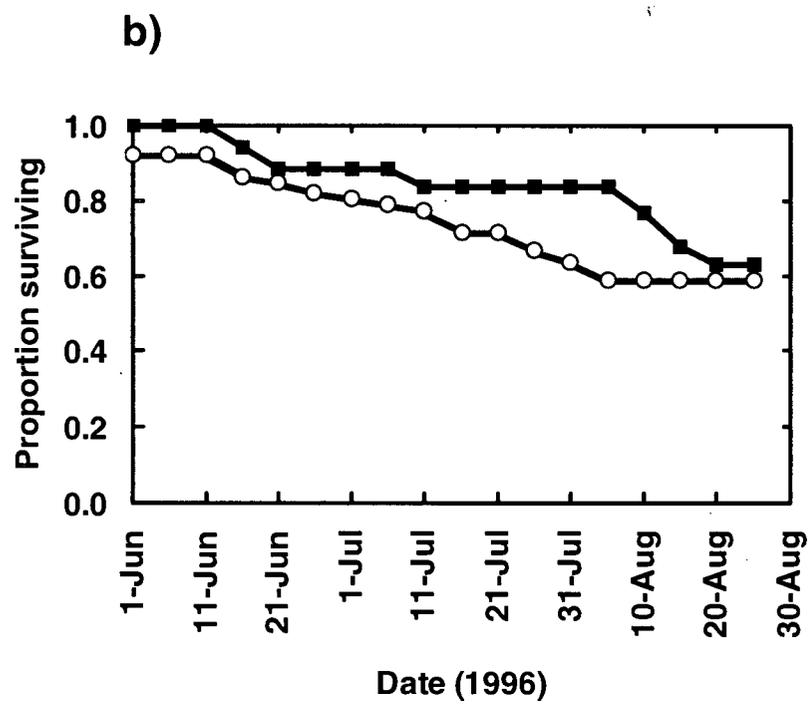
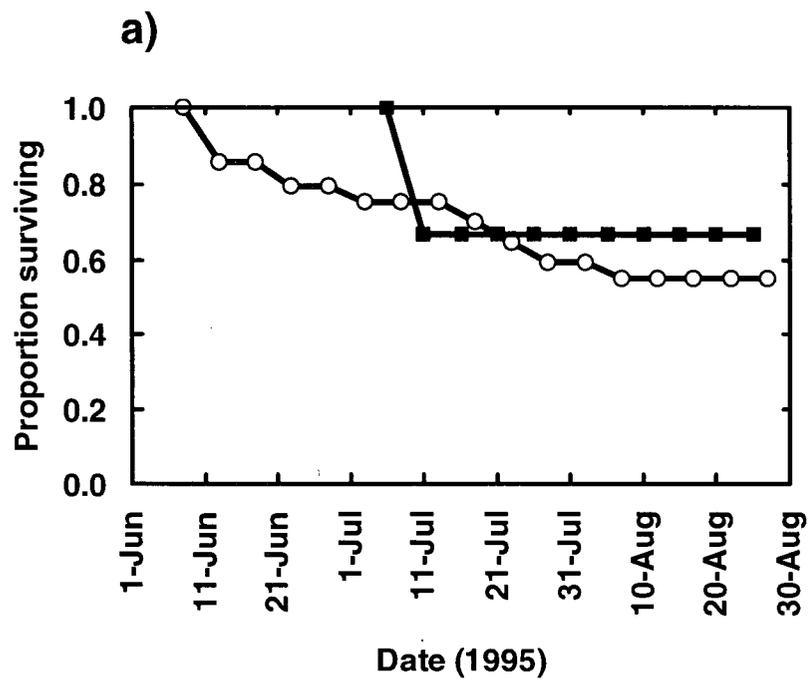
only in 1997 (1995: $\chi^2_2 = 2.0$, $p > 0.3$; 1996: $\chi^2_2 = 3.9$, $p > 0.1$; 1997: $\chi^2_2 = 6.8$, $p < 0.05$). In 1996 and 1997 only about 9% of the telemetered animals in the Exclosure died of causes other than predation, compared with less than 2% of Control animals. In 1996 the proportions of animals known to have died of all causes combined were approximately equal within (25%) and outside (24%) the Exclosure.

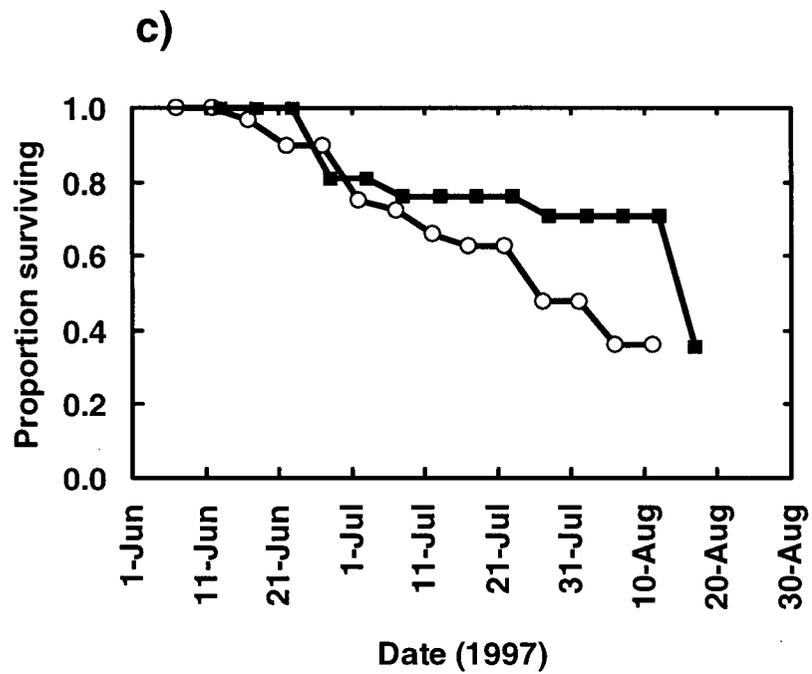
Although survivorship of adult and subadult *Dicrostonyx* (at least 28 g) estimated with Kaplan-Meier analyses of radio-telemetry data (Fig. 2-6) was generally higher within the Exclosure than on Control grids, the difference was significant in 1997 only (log-rank tests, 1995: $\chi^2_1 = 0.4$, $p > 0.5$; 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. 2-6, 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 (Fig. 2-7). 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 estimated 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 predation occurred within the protected area.

Comparison of results from the two methods

Analysis of our mark-recapture and radio-telemetry data led to different estimates of survival rates (Figs. 2-4, 2-7). The estimates from mark-recapture were generally lower and less precise than those from radio-telemetry, but mark-recapture estimates showed improved survival

Fig. 2-6. 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.





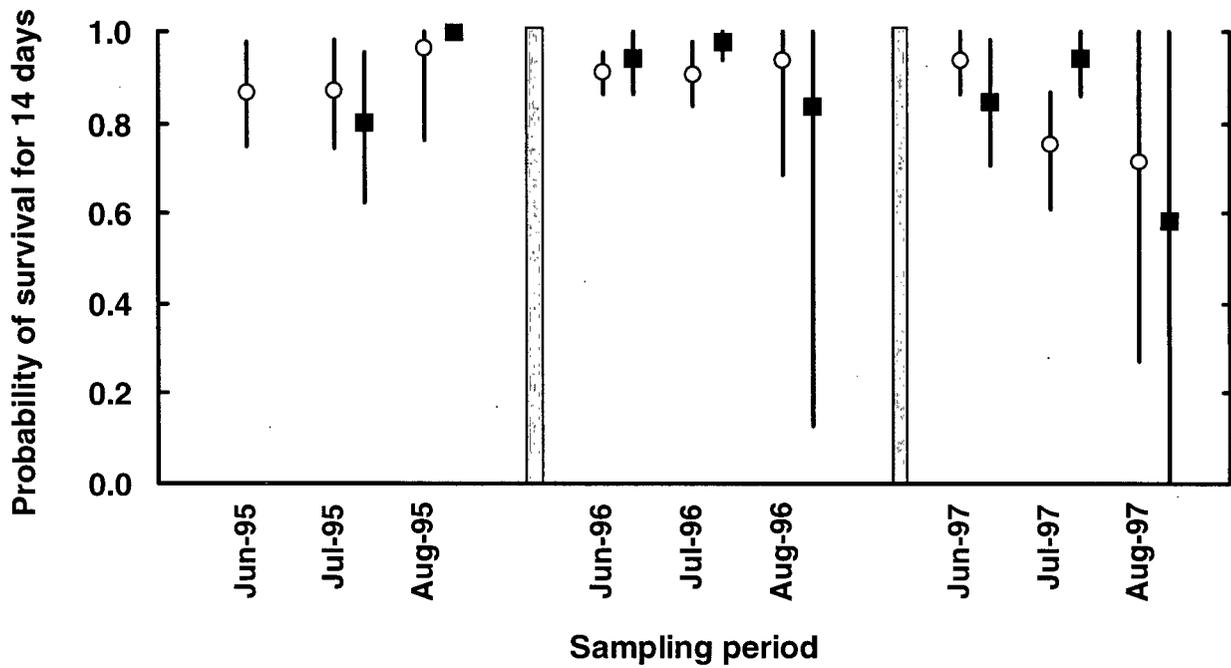


Fig. 2-7. Estimates and 95% confidence intervals of Kaplan-Meier 14-day survival of telemetered adult and subadult *Dicrostonyx* (weighing at least 28 g) on Control (open circles) and Exclosure (filled squares) grids in June, July, and August of 1995, 1996, and 1997.

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 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 small-scale 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 Chapter 3. 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. An example of the interpretation of such models is given under Age Structure below. 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

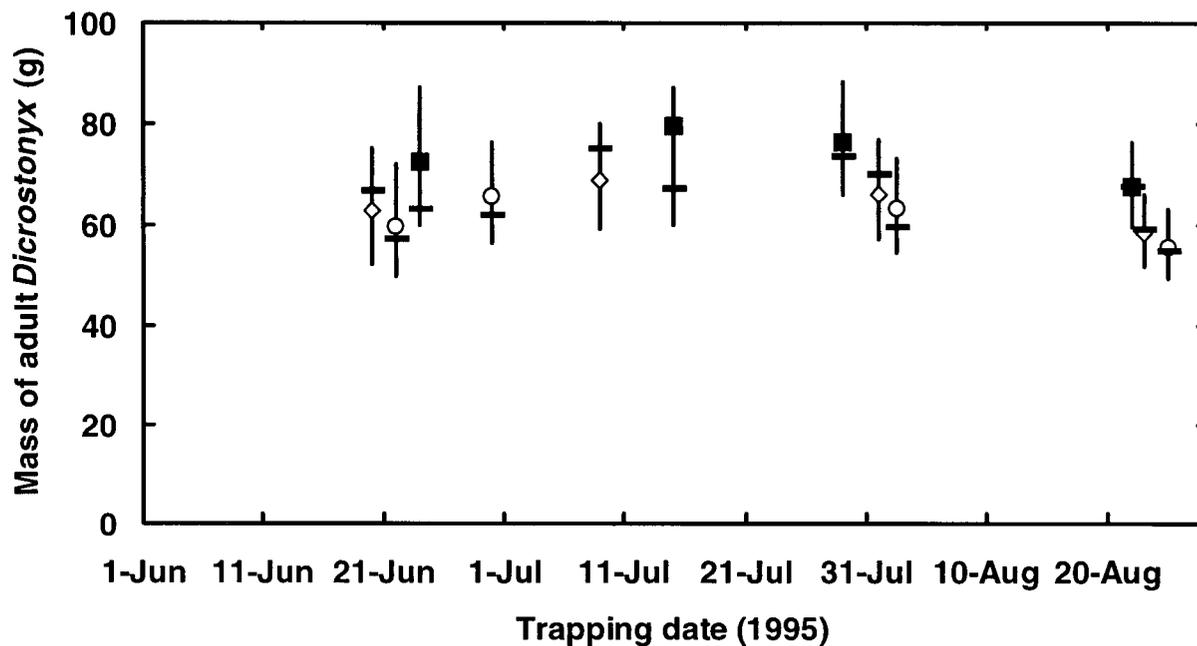
Trapping grid was not retained in the model relating sex ratio to year, period, and grid ($\Delta\text{AIC} = -0.18$); we conclude that the proportions of males and females did not differ significantly between the Exclosure and Control grids.

Mass of adults and juveniles

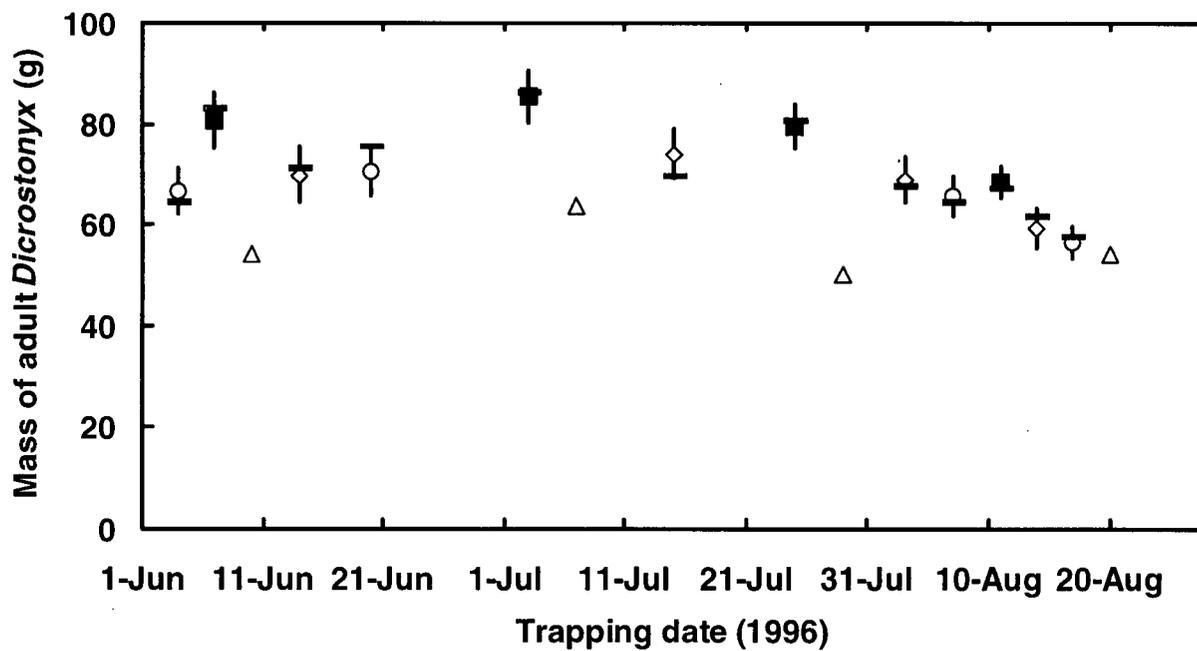
The average mass of animals classified as adults when first caught (weighing > 40 g) was greater in the Exclosure than on Control grids across all years (Fig. 2-8, $t_{697} = 9.9$, $p < 0.0001$) (see also Fig. 2-9). This pattern was true of both males and females ($t_{259} = 5.4$ and $t_{431} = 8.9$, $p < 0.0001$). The mean mass of males and females in the Exclosure across all years and periods was

Fig. 2-8. 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. weighed at least 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.

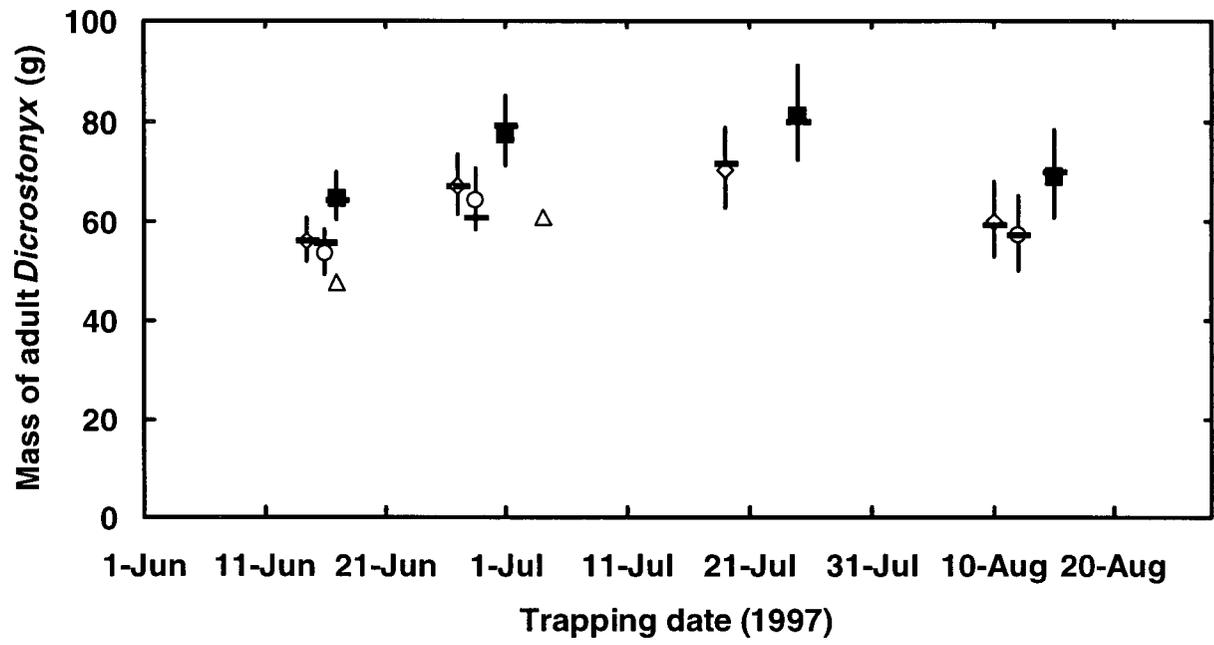
a)



b)



c)



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 predicted for the Exclosure (Fig. 2-8a).

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 July – August. 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.

Age structure of the populations

Histograms of the frequencies of animals of different mass (Fig. 2-9) show clearly that once the predator exclosure was completed in late July 1995, there was a higher proportion of heavy animals within the protected area than on Control grids. There was also a smaller proportion of juvenile animals (≤ 40 g) within the Exclosure than on Control grids throughout 1996 and in June and early July 1997. For example, in August 1996 55 of 176 (31%) animals on Control grids weighed ≤ 40 g, whereas only 15 of 145 (10%) animals in the Exclosure did so. This effect was not apparent in 1995 nor in late July or August 1997. In August 1997 there was a higher frequency of juveniles within the Exclosure than outside (see also following paragraph).

In the model of proportions of adults as a function of year, period, and grid, there were interactions between year and grid. Therefore we analysed the data from the three years separately, and included the third Control grid in models of the data from 1996 and 1997. Table 2-4 shows the coefficients of the model fitted to the 1996 data. The interaction between grid and

Fig. 2-9. Histograms of the frequency of *Dicrostonyx* of different mass, on the Exclosure grid and all Control grids combined, in August 1995, June 1996, August 1996, June 1997, and August 1997. The label below each bar represents the midpoint of the range; e.g. the bar labelled 35 includes animals of mass > 30 g and ≤ 40 g. Numerals above each histogram indicate the sample size.

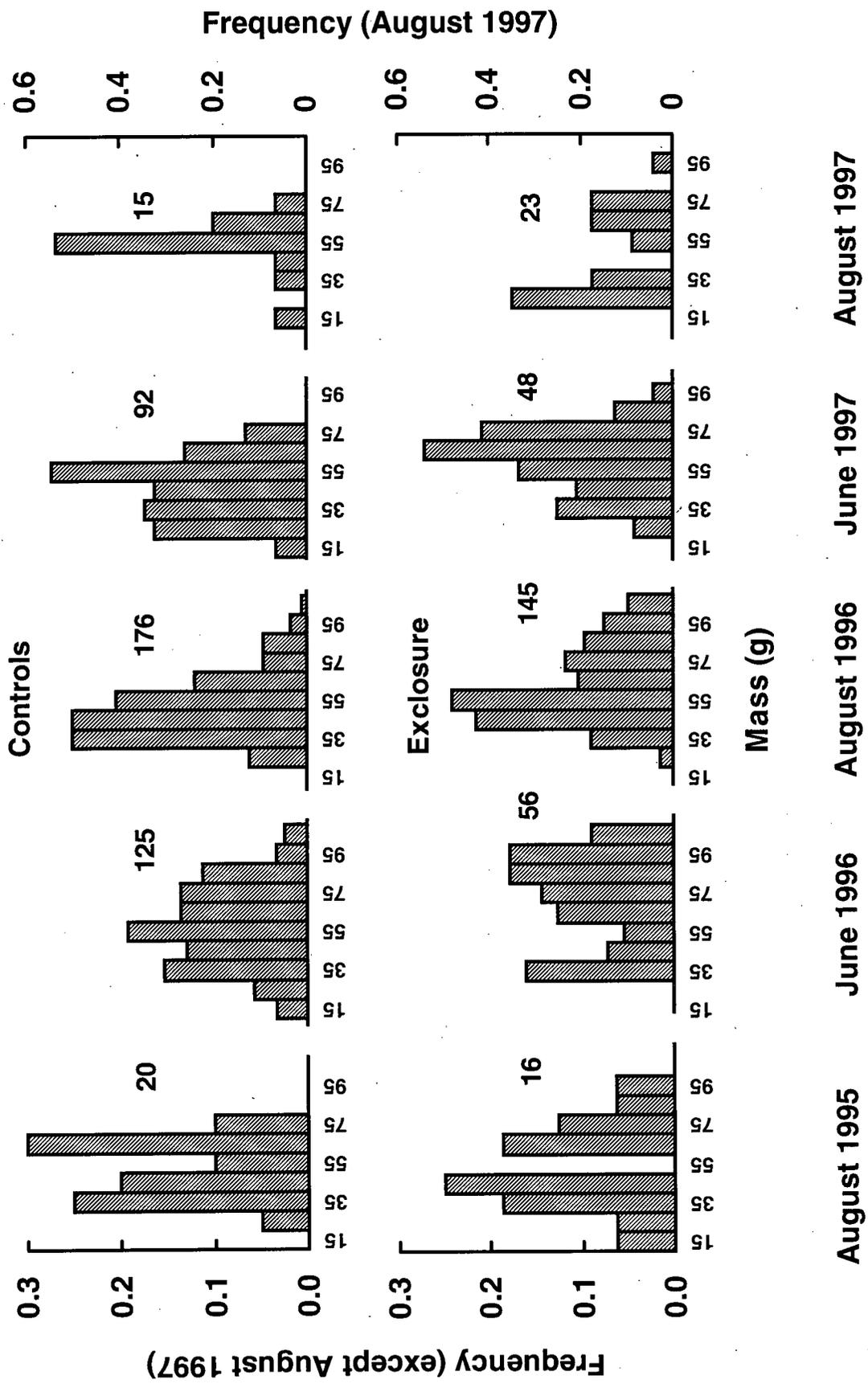


Table 2-4. Coefficients of the logistic regression model of the proportion of *Dicrostonyx* classified as adult when first caught, in 1996. Coefficients for time periods are compared by means of t-tests to that for August (treatment contrasts). Grids were compared with Helmert contrasts; hence the t-test for the Exclosure coefficient compares it with the mean of the coefficients for the 3 Control grids.

	Value	SE	t	p <
Intercept	0.32	0.12	2.63	
Period: June	0.46	0.23	2.00	0.05
Period: June-July	0.93	0.22	4.18	0.0001
Period: July-August	-0.49	0.17	-2.98	0.005
Grid: Control 2	0.37	0.11	3.43	0.001
Grid: Control 3	0.08	0.07	1.25	0.3
Grid: Exclosure	0.18	0.04	4.94	0.0001

Null Deviance: 1244 on 935 degrees of freedom

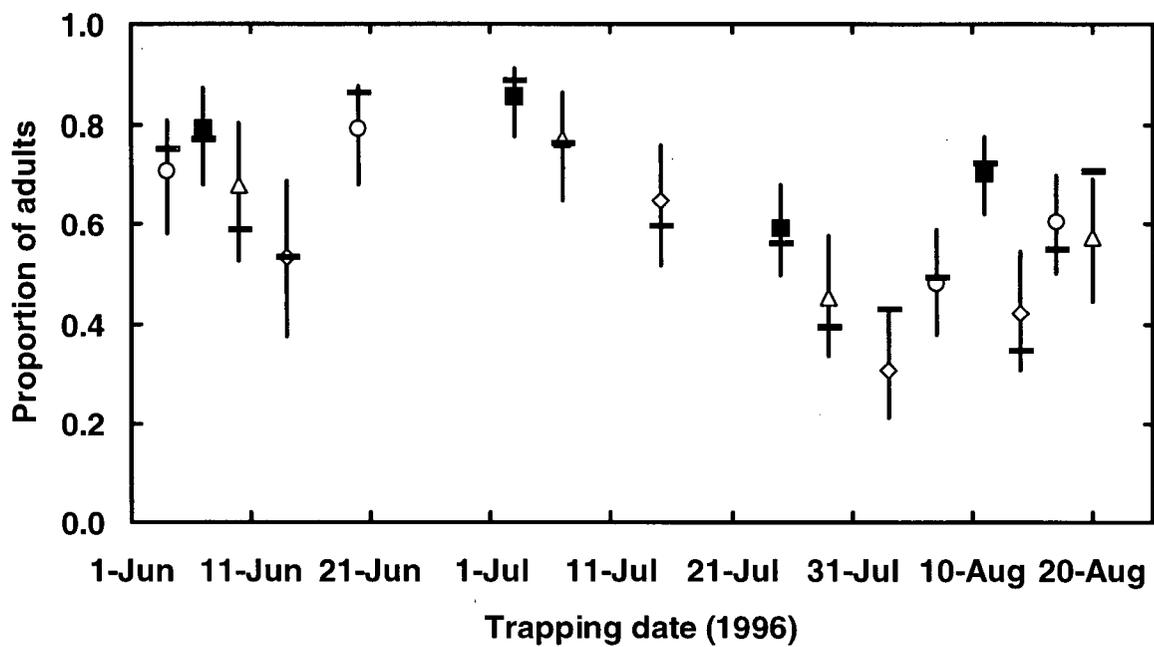
Residual Deviance: 1165 on 929 degrees of freedom

period did not remain in the model. The value of each coefficient is the estimated difference in the probability, q (on a logit scale: $\text{logit}(q) = \ln[q/(1-q)]$), of a *Dicrostonyx* being an adult, relative to a reference grid and sampling period. The coefficient for each period was calculated relative to August (treatment contrasts). For example, the $\text{logit}(\text{probability})$ of an animal caught in late June to early July being an adult was 0.93 greater than that of an animal caught in August being an adult. This difference was significantly different from 0 ($t_{929} = 4.2$, $p < 0.0001$). The parameter for each grid was fitted relative to the mean of the grids previously entered into the model (Helmert contrasts). Thus, the $\text{logit}(\text{probability})$ of an animal caught in the Exclosure being an adult was 0.18 greater than the mean probability on the other three grids ($t_{929} = 4.9$, $p < 0.0001$). The residual deviance approximately corresponded with the degrees of freedom, which suggests a satisfactory fit (Venables and Ripley 1997, p. 235). The actual proportion of adults across all periods in 1996 was 70% in the Exclosure, compared with 56% on all Control grids (Fig. 2-10a).

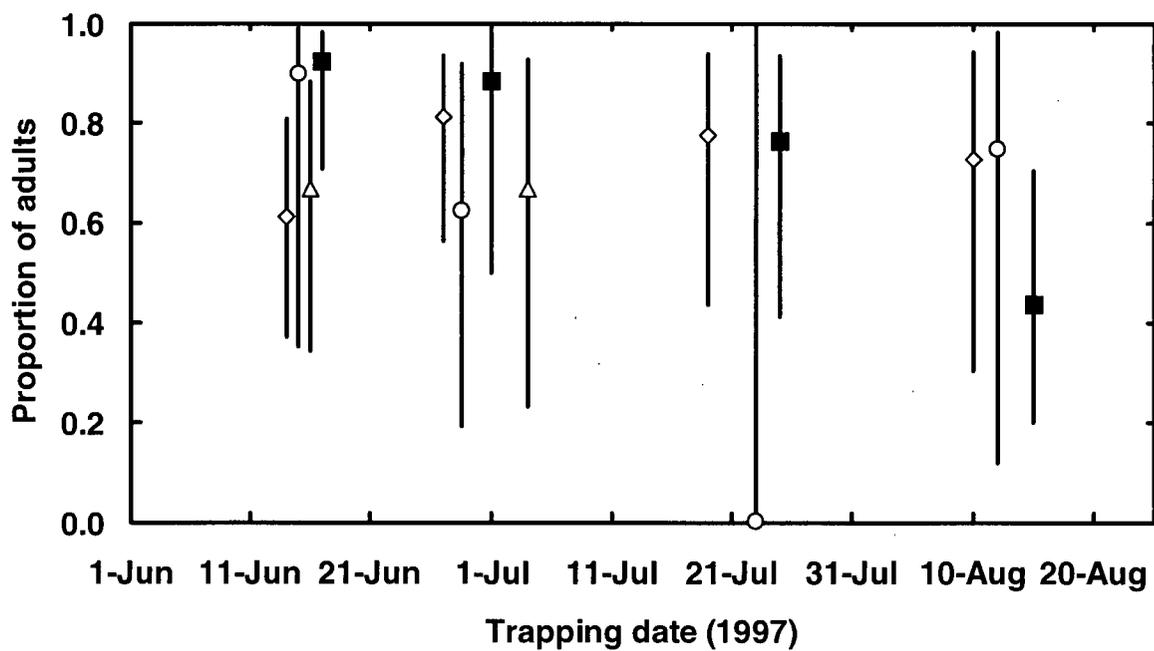
In 1995 the difference between the Exclosure and the Control grids was in the other direction and was not statistically significant ($t_{81} = -0.23$, $p > 0.8$). In 1997 there was a significant interaction between period and grid; as the season progressed the proportion of adults in the Exclosure declined whereas the proportions on the other grids stayed relatively constant (Fig. 2-10b). Relative to August, the difference in the probability of being an adult between the Exclosure and Control grids 1 and 2 was greater (more positive) in both June ($t_{224} = 2.16$, $p < 0.05$) and June-July ($t_{224} = 1.99$, $p < 0.05$). (Control grid 3 was not included in these comparisons because of missing data late in the season.) In August 1997 there was a higher proportion of juveniles in the Exclosure than on the Control grids although the difference was not statistically significant ($t_{35} = -1.65$, $p = 0.11$). In the last trapping session of 1997 only 2 of 16 *Dicrostonyx* caught on the two Control grids, but 12 of 23 caught in the Exclosure, weighed less than 40 g.

Fig. 2-10. Age structure of populations of *Dicrostonyx groenlandicus* in (a) 1996 and (b) 1997 on Control (diamonds, circles and triangles) and Exclosure (squares) grids. Points show the proportions of adult animals (> 40 g when first captured) estimated with logistic regression models. Error bars represent 95% confidence intervals. Horizontal lines in (a) show the actual proportions of adults captured during each time period on each grid. Lines are not shown in (b) because the predicted means matched the observed proportions exactly, owing to an interaction term in the model.

a)



b)



The proportions of adults captured fell within the 95% confidence intervals of the probabilities estimated by the models in all instances except Control grid 3 in August 1996 (Fig. 2-10a, b). Because the interaction term was retained in the model of the data from 1997, the fitted means matched the observed proportions exactly. The greater proportion of adults in the Exclosure than on Control grids in 1996 is evident both from the data and from the model's estimates. The same pattern was apparent early in 1997 until the proportion of adults began to decline in the Exclosure.

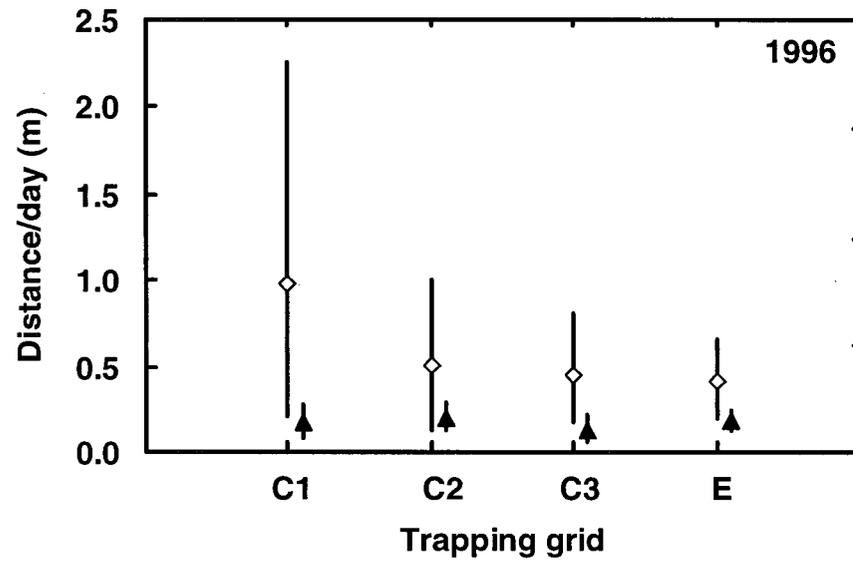
Movements of lemmings

In 1996, both male and female *Dicrostonyx* weighing at least 25 g showed net displacements of less than 1 m day⁻¹, on average, between trap sessions. There were no significant differences among trapping grids (Fig. 2-11a). In 1997, males showed net displacements of an average of about 5 m day⁻¹ between trap sessions, and females about 2 m day⁻¹. Again, there were no significant differences among grids (Fig. 2-11b). 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.

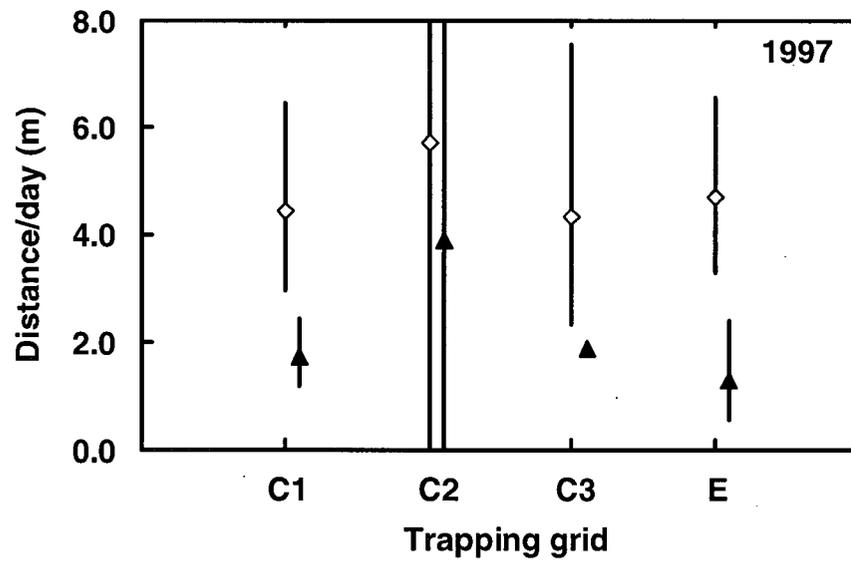
The fence around the Exclosure was permeable to lemmings and we observed runways crossing it. In 1996 and 1997 some telemetered lemmings moved outside the Exclosure although the fence was a minimum of 25 m from the edge of the trapping grid. In 1995 no telemetered animals left the Exclosure even though the fence was not finished until August. In 1996 only one animal, a male, did so, compared with 3 Control animals (2 females and 1 male) that moved more than 25 m from the edges of their grids. In 1997, one male and one female moved outside the Exclosure, compared with 5 males that left Control grids. Since 2.5 and 1.7 times as many Control lemmings as Exclosure lemmings were radio-collared in 1996 and 1997 respectively (Table 2-3), the number of Exclosure animals that crossed the fence was not lower than expected

Fig. 2-11. 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).

a)



b)



relative to the movements of Control animals (log-linear analysis of 3-dimensional $2 \times 2 \times 2$ contingency table, $\chi^2_2 = 0.18$, $p > 0.9$). The female that left the protected area in 1997 later re-entered and then went back outside.

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.* in press). 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 m²) 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 days and a 20-g male moved 41 m in 5 days. In 1997 a sexually mature 35-g male moved 250 m in 12 days, and a 17-g male tagged at the research camp was trapped 21 days 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 2-3). Of the juveniles with glue-on radios, which fell off and were retrieved within 3 – 7 days, the fates of 29 from the above study and 14 not previously reported are shown in Table 2-5. 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 ($\chi^2_2 = 12$, $p < 0.005$).

Table 2-5. Fates of immature *Dicrostonyx* fitted with glue-on radios, including 29 individuals reported by Blackburn *et al.* (in press) 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

DISCUSSION

In the following discussion we first examine alternative hypotheses to account for the observed increased mass of individuals and altered age structure of the population within the predator exclosure. We next conclude from our experimental and radio-telemetry results that predation was necessary to limit the density of *Dicrostonyx* during the peak and decline summers studied, but that the magnitude of the limitation was greater in the decline. We discuss the apparently contradictory results we obtained in the case of *Lemmus*. Finally, we describe effects of predation on the cyclic dynamics of the lemming population.

Effects of predator reduction on mass, age structure, and reproduction

Both male and female adults (animals weighing over 40 g when first caught) were larger within the Exclosure than outside throughout the experiment (Figs. 2-8, 2-9). 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, large individuals that had stopped growing remained in the population longer within the Exclosure than outside, and were not replaced during the summer. All the large adults we caught in June (Fig. 2-9) were over-wintered animals, born the previous summer or fall. Only one spring-born juvenile in 1996 and one in 1997 grew into the 81 – 90 g weight class (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 large 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 1993b). 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 the proportion of lemmings in reproductive condition was similar between the treatments, and since there was a reduced proportion of juveniles in the Exclosure in 1996 and early 1997 (Fig. 2-9, discussed further below). 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.

The age structure of the population of collared lemmings within the predator exclosure differed from that outside during the peak summer and in the early part of the decline summer. The proportion of animals classified as adults when first caught (≥ 40 g) was greater in the Exclosure than on Control grids (Fig. 2-10), and the proportion of juveniles caught at each trapping session (≤ 40 g) was smaller (Fig. 2-9). Possible hypotheses to account for these patterns are (1) density-dependent reproduction, (2) density-dependent dispersal of juveniles, (3) density-dependent infanticide, (4) a higher rate of predation on juveniles within the Exclosure, most likely by ermine, (5) an effect of different habitat in the Exclosure, (6) higher growth rates of juveniles protected from predation, and (7) the exclusion of juveniles from traps by large animals. We have evidence against most of these hypotheses. The first three incorporate density-dependence, and can be eliminated because the difference in age structure was apparent early in 1996 when the density in the Exclosure was similar to that on Control grids (Figs. 2-9, 2-10a). Density-dependent reproduction (hypothesis 1) is further refuted because we found no difference 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. Hypothesis (2), density-dependent juvenile dispersal, is further refuted because juveniles did not disperse from either the Exclosure or a Control grid during the peak summer (details in Results; Blackburn *et al.* in press). A higher predation rate on Exclosure juveniles (hypothesis 4) is refuted because the predation rate on juveniles during the peak seems to have instead been lower within the Exclosure than outside (Table 2-5). Hypothesis (5), differences in habitat, must be considered because the predator

exclosure treatment was not replicated in any year. However, if the difference in age structure between the treatments were a result of habitat differences, the observed patterns should have been evident throughout the study. Instead, the age structure difference was not apparent before the protective structure was completed in 1995 (Fig. 2-9) or late in the decline summer of 1997 (Figs. 2-8b, 2-10d). High growth rates of neonates within a predator exclosure (hypothesis 6) was observed by Reid (1995) and may occur as a result of reduced predation risk to lactating females (discussed below). However, the persistent reduction in captures of the smallest lemmings (≤ 20 g and 21 – 30 g) in the Exclosure is not consistent with this hypothesis unless the next is also true. Hypothesis (7), that larger adults in the Exclosure prevented juveniles from entering traps is not entirely satisfactory since the difference in age structure was apparent in June 1996 when densities were similar on all grids. However, since as discussed above, adults were on average larger and possibly older in the Exclosure than outside, they may have been more aggressive or more territorial. We do not know the reason for the difference in age structure between our experimental treatments; it remains an opportunity for further research.

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 all mortalities on Control grids were due proximately to predation. Second, density increased in the protected area more than on the Controls. Third, both mark-recapture and Kaplan-Meier estimates of survival within the Exclosure were higher than on Control grids in 1997. Fourth, although some compensatory mortality may have occurred it was not 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 other sources of mortality compensated for the reduced predation on radio-collared animals in the Exclosure, since the proportions of total mortalities were about equal between the Control and the Exclosure grids (Table 2-3). In 1996 mortality was low (Figs. 2-6b, 2-7); hence the predation rate was low. Therefore experimentally reducing predation, even if no compensatory mortality occurred, 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 2-5) 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 2-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 occurrence of compensatory mortality in the peak suggests that other loss factors such as disease might also be limiting then. However, the low survival rate (Figs. 2-6c, 2-7) and the lack of compensatory mortality during the decline (Table

2-3) 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 (Chapter 3), 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 1989), 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.* in press). 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, an increased proportion of juveniles, and either a greater proportion of animals in reproductive condition, or larger litter sizes. As discussed above, we did find larger animals in the protected area, but a smaller proportion of juveniles and no difference in the proportion of reproductive individuals. We have no data on litter sizes. In short, we cannot reject the RSF hypothesis; in our experiment reduced predation risk may have led to enhanced reproduction, resulting in an increase in density that was confounded with the increase in density resulting from enhanced survival. This potential secondary effect of predation represents an opportunity for further research.

Possible criticisms of the predator exclosure experiment

The increased density in 1996 without a significant increase in survival in the protected area makes it worth considering whether other factors could have enhanced the density of lemmings in the Exclosure. As discussed above, we cannot discount the possibility that the habitat was better there, because the treatment was not replicated within any year. However, if habitat were 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. 2-2). Our conclusion that the habitats were of equivalent quality between treatments is supported further by the lack of enhanced reproduction within the Exclosure, although we have no data on litter sizes. A second factor that could have increased density within the Exclosure is restricted emigration due to a partial fence effect (Krebs *et al.* 1969). This is unlikely because 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.* in press) 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.

Abundance and survival of brown lemmings

Since *Lemmus* prefer wet habitats (Rodgers and Lewis 1986b) where they feed primarily on sedges and grasses (Rodgers and Lewis 1986a), their increase on our study grids in the peak year may have been in part a result of emigration from overpopulated preferred habitats. *Lemmus* were most abundant on Control 1 grid, which had the largest area of wet habitat, but they were caught in drier parts of the grids also. In July 1995 and 1996 approximately equal numbers of *Dicrostonyx* and *Lemmus* were caught in snap-trap lines that traversed both hummocky and sedge-grass habitats (4 of each in 1995, 28 *Dicrostonyx* and 24 *Lemmus* in 1996, but 4 *Dicrostonyx* only in 1997; R.G. Bromley, pers. comm.).

Protection from predators had no apparent effect on abundance or survival of *Lemmus*, perhaps owing to a combination of small sample size and immigration of *Lemmus* from adjacent areas. As well, *Lemmus*, which are aggressive and run fast, may be less vulnerable to predation than are *Dicrostonyx*. *Lemmus* may not have been limited by predation in the hummocky areas, but we cannot draw conclusions about their population dynamics in sedge-grass habitats.

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. 2-7) and a larger proportion of animals died as a result of predation (Table 2-3). A low predation rate at very high prey density is predicted when the functional and numerical responses

of predators are asymptotic (Holling 1959a). 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, Korpimäki *et al.* 1991, Korpimäki 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. We did not observe a delayed numerical response of arctic foxes (Chapter 4). The survival rate of radio-collared animals on Control plots tended to decrease as the population declined in the summer of 1997 (Fig. 2-7). During the same period, the difference in density between the Exclosure and Control grids increased (Fig. 2-2). These trends imply an inversely density-dependent (depensatory) predation rate during the decline phase of the cycle. 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 1959a).

Implications for lemming population dynamics

Five 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, other sources of mortality compensated for predation mortality within the experimental predator exclosure, hence disease or other mortality factors might depress peak density in the absence of predation. Third, 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 exclosure (Fig. 2-2); that is, the decline was

reversed within our experimental treatment. Fourth, our finding of a higher predation rate during the decline phase than during the peak shows that predation accelerates the decline, as proposed by Pearson (1971); the increased proportion of losses in the decline relative to the peak phase results in a steeper negative rate of population change than would occur in the absence of predation. Fifth, 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).

Our results indicate that predation alters the amplitude and period of the lemming population cycle, but without autumn and winter data they cannot show whether predation caused the population decline. The only predators present in winter are arctic foxes, snowy owls, and ermine. In Chapter 3 I compare indicators of reproduction among years and analyse predator numbers and diets to examine the role of these predators in initiating the decline.

CHAPTER THREE

PREDATION AND THE DECLINE OF COLLARED LEMMING POPULATIONS

INTRODUCTION

What pushes a growing population into a decline? This question has been a recurring focus of attempts to explain fluctuations in the population density of lemmings and other small mammals (reviewed by Krebs and Myers 1974, Stenseth and Ims 1993b). Predation is one of many hypotheses advanced to explain declines. This hypothesis has not been tested experimentally in lemmings, but Korpimäki and Norrdahl (1998) halted a summer decline in vole populations by removing predators. Even so, the direct effects of predation alone may not be enough to initiate a decline from high density. A mortality factor that triggers a decline in a cyclic population must act in a delayed density-dependent manner, leading to a higher per capita mortality rate during the decline than during the peak phase of the cycle. But because the number of predators in an area and their rate of prey consumption are limited they may have little impact on a high-density prey population. Lack (1954) suggested predation could not cause a decline without a decrease in reproduction as a result of food shortage, but evidence of starvation in the peak phase has not been found. Henttonen *et al.* (1987) proposed that declines in microtine populations might involve predation, an extrinsic factor, combined with intrinsic factors that slow population growth. Many researchers now agree that population cycles in small mammals may result from an interaction between intrinsic and extrinsic factors (e.g. Krebs 1996, Stenseth *et al.* 1996).

At Walker Bay on the Kent Peninsula, N.W.T., the collared lemming (*Dicrostonyx groenlandicus*) population declined from August 1996 to August 1997. By experimentally

reducing predation on an 11-ha area of tundra and using radio-telemetry to determine the fates of collared lemmings, I showed that predation limited the lemming population during both the peak (1996) and the decline (1997) summers (Chapter 2). In the summer of 1997, density rose in the protected area while the decline continued elsewhere (Chapter 2). However, much of the population decline occurred in autumn and winter, when I was neither trapping nor monitoring lemming survival, and the enclosure was less effective because snow covered the fence. Did predation cause the population decline in fall and winter?

I compared rates of survival between the peak (1996) and decline (1997) summers, examined evidence of winter predation (1996 – 1997), and compared rates of decline between the protected and control populations to test the hypothesis that predation was a necessary cause of the lemming population decline. I tested three predictions of this hypothesis: (1) the lemming population will not decline in an area protected from predation when it declines on unprotected sites, (2) the predation rate on lemmings is delayed density-dependent, and (3) the population decline is associated with an increase in predation rate. Since the rate of decline is affected by reproductive rate, I also compared indicators of reproduction among years. I used simple population models to test whether the observed demographic rates would lead to the observed decline.

METHODS

I live-trapped lemmings on three Control grids and on one "Exclosure" grid that was protected from predators (9 ha per grid) at Walker Bay on the Kent Peninsula, N.W.T., in the summers of 1994 – 1997 (Chapter 2). The density of lemmings was very low in 1994, increased in 1995, was high in 1996, and declined in 1997. Details of density estimation with mark-recapture analyses, survival estimation with radio-telemetry, and assessment and statistical

analyses of mass and reproductive condition, are given in Chapter 2. I also used snap-traps to survey the relative abundance (Chapter 4) and reproductive condition of lemmings, in June 1996 – 1997 and July 1994 – 1997. I caught collared lemmings (*Dicrostonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) with both methods. However, because collared lemmings were most abundant and brown lemmings were found in large numbers only in 1996, I discuss only collared lemmings in this chapter.

Numerical response of predators

I recorded all known dens, nests, and when possible litter or clutch sizes of predators. Others and I regularly visited or systematically searched an area of approximately 35 km² (the “study area”) in the course of research on geese (Bromley *et al.* 1995 and Chapter 4), lemmings (Chapter 2) and predators (this chapter). I found most fox dens and nests by observing the movements of predators, or by chance. Each spring and periodically in summer I visited all previously known fox dens to determine which were active. Once or twice each summer I searched systematically for raptor (rough-legged hawk and peregrine falcon) nests along a line of cliffs running approximately north – south about 3 – 5 km east of our study grids (snowy owl nests were also found in this area in 1996). These searches were done on foot each year and by helicopter once in each of 1995 and 1996. I did not search systematically for ermine dens in summer, and found them by chance only. Because glaucous gulls nested on islands that were difficult to reach, I have no data of the breeding of gulls. Territorial pairs of pomarine jaegers were counted in summer 1996 in a helicopter survey of 11.2 km² within the study area (Chapter 4). Nests of sandhill cranes were recorded during annual ground searches (10 – 12 km²) for goose nests in and near the study area (Bromley *et al.* 1995).

Winter nests of ermine

In winter, lemmings build nests of grass and other plant material on the surface of the ground under the snow. When an ermine kills a lemming it sometimes occupies its winter nest and lines the nest with lemming fur (MacLean *et al.* 1974). Each year I searched some of the trapping grids for evidence of winter ermine predation. I counted winter nests each summer by walking parallel transects 6 m apart across a grid and recording and then destroying all nests found. I considered nests lined with fur and containing ermine scats to have been occupied by ermine, but not nests with only a trace of fur (Sittler 1995). I did not search the vicinity of the nests for ermine scats. I assumed that very flattened, decomposing nests were from a previous year and did not count them; this assumption may have led to errors, particularly in the first year (1994) of the survey (Sittler 1995).

Diets of predators – analysis of fox scats

Each summer I collected fresh arctic fox scats periodically from dens and opportunistically from elsewhere. I also collected scats from the snow each spring beginning in 1995. Each scat was bagged and, if wet, frozen for later analysis. In years when sample sizes were large enough, I grouped scats according to sampling periods approximately corresponding to dates when I had estimates of lemming population density. Samples collected from the snow were grouped as “winter scats”. I used the method of Reid *et al.* (1997) to distinguish scats of adult and juvenile foxes according to their diameter. From each period I analysed up to 30 adult scats and 19 juvenile scats when the latter were available. In order to maximise the independence of the samples within each period, I selected all opportunistically collected scats, and randomly chose equal numbers of scats from each den from which they had been collected during that period. My method of analysis of scat composition generally followed that of Reid *et*

al. (1997) except that I focussed on lemmings in the diet rather than on the entire diet. Details are given in Appendix 1.

Functional response of foxes

I plotted the functional response of foxes to lemming density as the number of lemmings consumed per fox (adults and juveniles) per day against the mean density estimated by mark-recapture (Chapter 2) during the period. I fitted a curve to the adult fox data, with the form

$$\text{Attacks} = \frac{aN^m}{1 + ahN^m} \quad (1)$$

When the exponent $m = 1$, this is Holling's (1959b) disc equation for a Type II functional response, where Attacks is the number of attacks on the prey per unit of time; a is the predator's rate of effective search for that prey, h is handling time, and N is prey density. If $m > 1$, the curve is sigmoid, as in a Type III response. The curve was fitted with JMP IN software's non-linear fit routine (Sall and Lehman 1996), by minimising the residual (error) sum of squares.

Mortality rate of lemmings from radio-telemetry data

I used Kaplan-Meier analysis of radio-telemetry data to estimate the mortality rate due to fox predation alone, using the methods described in Chapter 2. I compared these mortality rates with those estimated from the total response of foxes to lemming density (observed functional response \times observed numerical response \div prey density).

Analysis of pellets from avian predators

I gathered fresh raptor pellets from rock perches and from below nests periodically throughout each summer. I collected pomarine jaeger pellets opportunistically in 1996, and

short-eared owl pellets from where owls had killed telemetered lemmings in 1995. I obtained a few gull pellets from an island colony and from a ridge where gulls perched. To estimate winter diet, I also collected snowy owl pellets from the snow in spring 1997. Because my sample sizes were too small for me to group pellets from different periods within each summer, I estimated the number of lemmings per pellet for each species of avian predator in each summer for which I had samples, and for snowy owls in winter 1996 – 1997 (Appendix 2).

Functional responses of rough-legged hawks and snowy owls

I plotted the functional responses of rough-legged hawks and snowy owls to lemming density as the number of lemmings consumed per bird per day against the mean density estimated with mark-recapture (Chapter 2) during the period. Because there were few data (5 for owls and 3 for hawks) especially from low densities, I did not attempt to fit functional response curves.

Reproductive data from live-trapping

I assessed the reproductive condition of lemmings caught in live-traps (Chapter 2). I classified males as reproductive if their testes were scrotal, and females if the pubic symphysis was at least slightly open or the nipples enlarged, or if they were obviously pregnant. Beginning in July 1996 I recorded oestrus (perforate vagina) as a separate indicator of female reproductive condition, but because of differences in assessment among field workers I could not compare rates of oestrus among years. Only one *Dicrostonyx* was caught in 1994, in August; this animal is not included in the analyses reported below.

Reproductive data from snap-trapping

I dissected lemmings caught in snap-trap surveys to determine the reproductive status of females and males. For females I recorded pregnancy, number and size of embryos, and presence or absence of placental scars from previous pregnancies (scars were not recorded in June 1996). I considered that embryos much smaller than the others in a litter were being resorbed (Krebs 1964a) and excluded them from estimates of litter size. For males I recorded whether the epididymis was visible, as an indication of spermatogenesis. No lemmings were caught in snap-trap surveys in 1994.

Population decline models

I built a simple, deterministic population model (Fig. 3-1) in Microsoft Excel to compute winter population trajectories with different survival rates. I assumed that no reproduction occurred in the fall and winter (mid-August – mid-March) following the peak summer (Krebs 1964a, Chernyavski 1979). Chernyavski (1979) concluded that the reproductive rate was low in the spring of a decline on Wrangel Island, because of a low frequency of females with placental scars and a paucity of small animals trapped in June. Chernyavski and Kiriushchenko (1979) concluded, using the same data, that only one litter was born under the snow in the spring of the decline, in March, whereas in the increase year an additional spring litter was born in April. However, although none of the animals dissected at Walker Bay in June 1997 had placental scars (see Results, Table 3-14), I caught many small and medium-sized lemmings in June 1997. Forty-two percent caught in snap-traps weighed between 25 and 50 g (one weighed 29 g, all others > 30g; see Results, Table 3-15), and 20% of live-trapped Control animals were ≤ 30 g and 34% were between 30 and 50 g; Chapter 2, Fig. 2-9). Animals weighing 30 g are about 1 month old, and those 30 – 50 g are between 1 and 3 months old (Chernyavski and Kiriushchenko 1979). Krebs (1964) also caught only 1 female with placental scars ($n = 27$) in a decline year, although

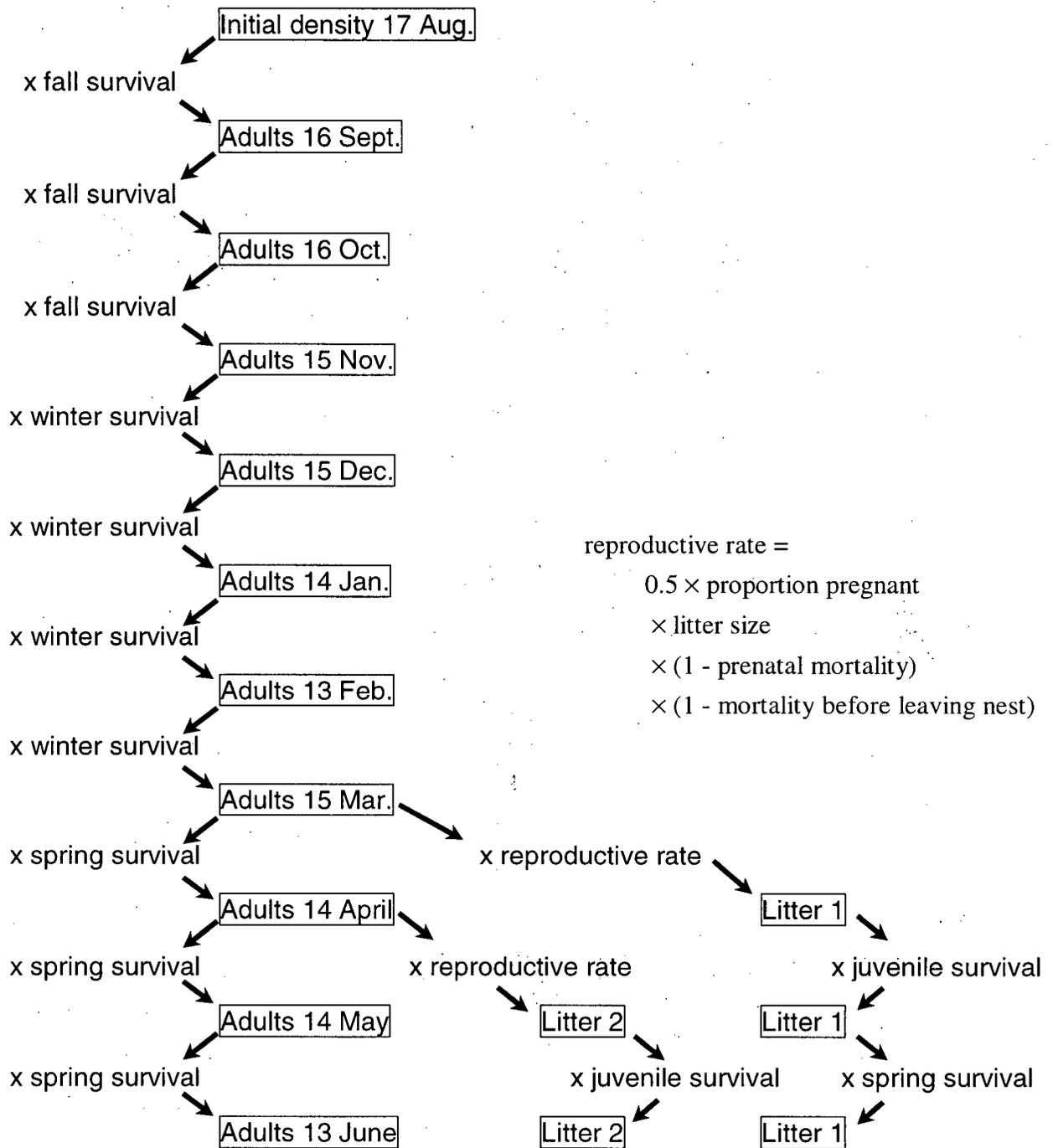


Fig. 3-1. Flow diagram of population decline model. Parameters are shown in Tables 3-1 to 3-3; survival and initial density parameters are described in Methods. Values in boxes show densities of *Dicrostonyx*. Steps are in increments of 30 days. The factor 0.5 in the reproductive rate represents a sex ratio of 1:1.

the females he collected in spring were pregnant (1 in each of April and May). From the size of the animals trapped, I assumed lemmings were born under the snow in two periods, March – April and April – May. I set the sex ratio of adults in 1996 to 1:1, and arbitrarily assumed that 30% of over-wintered females reproduced during each spring reproduction period, but that no spring-born animals reproduced in spring (Chernyavski *et al.* 1981).

In the first spring reproduction period I used a mean litter size of 3.8 (Chernyavski 1979) and for the second period I used 4.0 (Krebs 1964a, based on 1 female caught in May). I assumed that the rate of pre-natal, post-implantation mortality (resorbed embryos) was 0.063 and that 5.2% of juveniles died before leaving the nest about 14 days after birth (based on an increase year, Chernyavski and Kiriushchenko 1979). I set juvenile survival in the first month after leaving the nest to 0.63 (based on a peak year, Chernyavski and Kiriushchenko 1979). These juvenile survival rates are high; other estimates suggest much greater juvenile mortality in a decline year. Chernyavski and Kiriushchenko (1979) estimated that in a peak year 33% of neonates died before leaving the nest. Krebs (1964) estimated 28-day survival rates from birth to first trapping date (28 or 29 days of age) at 0.38 in the first summer litter of the peak, 0.05 in the first summer litter of the decline, and 0.28 in the first summer litter of an increase year. I assumed that juvenile survival in the second month after weaning was equal to the adult survival rate. Lemmings may temporarily cease to breed during or before snowmelt about May – June (Chernyavski and Kiriushchenko 1979, Batzli *et al.* 1980). Births occurred in June at Walker Bay, but I did not model juveniles born in June because most would not have been trappable in my June live-trapping sessions. These parameters are summarised in Table 3-1.

I tested several adult survival rates in the model. First, I used an autumn survival rate from mid-August to mid-November, before deep snow cover makes lemmings less vulnerable to foxes and snowy owls. The density of foxes and owls may be highest during this period; they may disperse or die as lemming numbers decline and winter conditions set in. Second, I used a

Table 3-1. Parameters of reproduction and juvenile survival used in the deterministic Microsoft Excel model of population decline. Distributions were used in the stochastic Crystal Ball model; when a normal distribution was assumed, the mean was set to the “estimate”. In most cases, only the estimate was published in the cited source; * indicates the only instance in which the standard deviation was also published. Details in Methods.

Parameter	Estimate	Distribution	Source
Winter reproduction	0	Constant	1, 2
Spring reproduction			
Litter size, March-April	3.8	Normal, SD = 0.85	2*
Litter size, April-May	4.0	Normal, SD = 0.9	1
Proportion of females breeding in each period	0.3	Uniform, range 0.1 – 0.5	4
Early juvenile mortality (proportion dying)			
Pre-natal, post-implantation	0.063	Normal, SD = 0.02	3
Before leaving nest	0.052	Normal, SD = 0.017	3
Juvenile survival per 30 days			
First month after leaving nest	0.63	Uniform, range 0.04 – 0.63	1, 3

Sources:

- 1) Krebs (1964)
- 2) Chernyavski (1979)
- 3) Chernyavski and Kiriushchenko (1979)
- 4) based on my data, see text

* both mean and standard deviation (SD) are from this source

winter survival rate from mid-November to mid-March. Third, I used a spring survival rate from mid-March to mid-June, when days lengthen and snow softens. In the initial run of the model I set the autumn and winter survival rates to the rate estimated from radio-telemetry in August 1996 and the spring survival rate to that estimated in June 1997 (Chapter 2). I used 30-day survival estimates based on the 14-day estimates reported in Chapter 2 (Table 3-2, this chapter).

The models were initialised with population densities estimated from mark-recapture data (Chapter 2). In the case of Control grids I calculated the mean of the three Control densities in each of August 1996 and June 1997 (Table 3-2). The start date for Control grids, 17 August, was the mean trapping date on Control grids in August 1996, and the time-step used in the model was 30 days. I then extrapolated the forecasted density on 13 June to 16 June, the mean trapping date on Control grids in June 1997, by multiplying adult and juvenile densities by the spring survival rate. Similarly, actual and modelled dates for the Exclosure were 11 August to 17 June.

Between trapping sessions in mid-August 1996 and mid-June 1997, the populations on the three Control grids declined at a mean rate of change (r) of -0.042 per week (SE: 0.016). Estimating the rate of decline as the weekly rate of change from the mean August 1996 density on Control grids to the mean June 1997 density on Control grids yields a similar r value, -0.036 per week. I used this latter rate for comparison to modelled results because of its straightforward relationship to mean density. The rate of change in the Exclosure was similar to the mean rate of change on Controls, -0.036 per week (Table 3-3).

I used Crystal Ball software, which interacts with Microsoft Excel as an "add-on", to forecast the effect of uncertainty in the parameter estimates. This program allows statistical distributions to be specified for each parameter and runs Monte Carlo simulations, randomly selecting parameters with the defined distributions (Decisioneering 1996). I used the same algorithm as in the deterministic Microsoft Excel model described above (Fig. 3-1). I defined adult survival parameters as normally distributed and set the means and 95% confidence limits

Table 3-2. Survival estimates (30 days⁻¹) of *Dicrostonyx* in 1996 and 1997, calculated from results of radio-telemetry studies reported in Chapter 2. Estimates for August 1996 and June 1997 were used in the population decline model. Other estimates and confidence intervals are shown for comparison.

<u>Year</u>	<u>Month</u>	<u>Estimate</u>	<u>95% confidence interval</u>
Control animals			
1996	June	0.820	0.730 – 0.909
	July	0.816	0.681 – 0.951
	August	0.876	0.445 – 1.0
1997	June	0.877	0.734 – 1.0
	July	0.546	0.348 – 0.740
	August	0.487	0.061 – 1.0
Exclosure animals			
1996	June	0.882	0.729 – 1.0
	July	0.952	0.869 – 1.0
	August	0.684	0.012 – 1.0
1997	June	0.703	0.477 – 0.963
	July	0.879	0.721 – 1.0
	August	0.315	0.0 – 1.0

Table 3-3. a) Estimated densities of *Dicrostonyx* (individuals ha⁻¹) in August 1996 and June 1997, on 3 Control grids and in the Exclosure, from Chapter 2. b) Rates of weekly population change during winter 1996-7 and summer 1997 on Control grids and in the Exclosure.

a) Density

<u>Trapping grid</u>	<u>Date</u>	<u>Density</u>	<u>95% confidence interval</u>
Control 1	14 August 1996	12.8	9.5 – 18.6
Control 2	17 August 1996	23.6	18.1 – 32.4
Control 3	20 August 1996	12.9	9.6 – 18.7
Mean Control density, August 1996		16.4	(S.D. 6.2)
Exclosure	11 August 1996	34.1	26.5 – 46.2
Control 1	15 June 1997	6.7	6.4 – 7.9
Control 2	15 June 1997	1.1	1.0 – 2.0
Control 3	17 June 1997	2.5	2.3 – 3.4
Mean Control density, June 1997		3.4	(S.D. 2.9)
Exclosure	17 June 1997	7.1	5.6 – 10.5

b) Rates of weekly population change (r)

August 1996 – June 1997

Mean rate of change on Control grids	-0.042 per week
Rate of change between mean Control grid densities	-0.036 per week
Rate of change in Exclosure	-0.036 per week

June 1997 – August 1997

Mean rate of change on Control grids	-0.192 per week
Rate of change between mean Control grid densities	-0.187 per week
Rate of change in Exclosure	+0.002 per week

for fall and winter survival to those estimated in August 1996, and for spring survival to those estimated in June 1997. Upper and lower limits for all survival parameters were set to 1 and 0. For initial density in August 1996 I assumed a normal distribution with the mean and standard deviation of the densities on the three Control grids (Table 3-3) and a lower limit of 0. For most other parameters I also assumed normal distributions (Table 3-1) with lower limits of 0. A standard deviation was available for only one parameter, March-April litter size (Chernyavski 1979). For April-May litter size I used a standard deviation in the same proportion to the mean (22%) as in the March-April case. For the parameters of juvenile pre-natal mortality and mortality in the nest I set the standard deviation to 33% of the mean. Because I have no data for the proportion of pregnant females in spring, I assumed a uniform distribution from 0.1 to 0.5. Different sources gave various estimates of juvenile survival in the first month of life or the first month after leaving the nest (see above; Krebs 1964a, Chernyavski and Kiriushchenko 1979); for survival in the first month after leaving the nest I used a uniform distribution covering the range of the published estimates (0.04 to 0.63 per 30 days).

To estimate the effect of variation in only the adult survival parameters, I ran a reduced Monte Carlo simulation model with all other parameters fixed at their estimated values (Table 3-1). I defined adult fall and winter survival parameters as described above but with the lower 95% confidence limit set to the lower limit estimated in July 1996 (because the August 95% lower confidence limit was very low).

I used Crystal Ball to obtain a sensitivity analysis of the full stochastic model. The program computes rank correlation coefficients between each parameter and the June density forecasted by the model. Each correlation coefficient is then squared and normalised to 100%, to indicate the approximate contribution made by each parameter to the total variance among forecasts (Decisioneering 1996).

RESULTS

Predation on telemetered *Dicrostonyx*

Most predation on telemetered lemmings was due to arctic foxes and ermine (Chapter 2, Tables 2-3 and 2-5). The only identified avian predators on telemetered lemmings were short-eared owls (in 1995 only) and pomarine jaegers (in 1996 only). Several mortalities were classified as due to unknown or suspected avian predators, and each year a large fraction of radios (and the lemmings wearing them) were lost, probably often due to predation (Chapter 2). However, although I checked for radios at nests, I knew of no telemetered lemmings killed by peregrine falcons, rough-legged hawks, or snowy owls.

Numerical response of foxes

Foxes bred in the 35-km² study area in 1995 (increase phase) and 1996 (peak phase), but not in 1994 (low phase) or 1997 (decline) (Table 3-4). The largest known litter sizes were 4 in 1995 and 11 in 1996. Den F1, which had 4 pups in 1995 and at least 4 in 1996, was within 2 km of Control 2 and 3 grids and the Exclosure, and within 3 km of Control 1 grid. This den was the closest successful den to all the trapping grids in 1995. In 1996, Den F5, which had 11 pups, was located on the ridge within 1 km of all the Control grids and less than 2 km from the Exclosure (Fig. 2-1). In 1995 this den was briefly occupied, but apparently the pups were later moved, about 0.6 km away to another den, which subsequently failed. Den F2, less than 1 km south of the Exclosure, was active in both years, with at least 2 pups in 1995 and at least 4 in 1996.

The behaviour of both adult and juvenile foxes appeared different in 1995 from that in 1996. In 1995 adults and pups at dens seemed lethargic: adults and older pups basked in the sun and often permitted observers to approach closely. In contrast, in 1996 adults barked and

Table 3-4. Numbers of known arctic fox dens and litter sizes within the 35 km² area that was regularly visited or searched in 1994 through 1997. In 1995 and 1996 I visited only 1 den often enough to be certain of the litter size (not the same den). "Minimum litter sizes" refers to litters at other dens where I saw or heard pups but may not have seen them all. In 1996 I knew of 4 other dens, one with at least 6 pups, outside this intensive study area but within 5 km of the lemming trapping grids.

Year	Dens	Known litter sizes	Other minimum litter sizes and notes
1994	0	—	
1995	5	4	2, 3 (+ 1 pup that died), 1 (this den was apparently moved to another location and subsequently failed)
1996	6	11	4, 4, 4, 1, 1 (4 known pups at one den and 1 known pup at another about 1 km away may have been parts of a single litter)
1997	0	—	

aggressively herded observers away from active dens, and pups ran and played and did not allow close approach. The lethargy of foxes in 1995 may have been the result of insufficient food.

To estimate how many lemmings these foxes could eat per unit area, I estimated the home range of foxes from published values. The typical summer home range of arctic foxes in Alaska is 20 km² (Eberhardt *et al.* 1982, Garrott and Eberhardt 1987), but estimates from other regions vary considerably. Home ranges were smaller in the Yukon-Kuskokwim Delta, where foxes live on birds and eggs (Anthony 1997), and on the coast of Iceland, where they eat birds, marine organisms, and carrion (Hersteinsson and Macdonald 1982, 1996), but larger on Svalbard, where they eat birds, seals, and carrion (Frafjord and Prestrud 1992, Prestrud 1992). Home ranges of individual foxes may overlap considerably, and a pair may share the same range (Frafjord and Prestrud 1992, Anthony 1997). On Svalbard, home ranges were often slightly smaller in fall and winter than in summer (Frafjord and Prestrud 1992). I assumed that a pair of foxes would forage over 25 km² to feed themselves and their offspring. I considered the 5 km x 5 km area centred on fox den F5, located on the ridge less than 2 km from all grids. I estimated by eye from a satellite map that this area included about 55% *Dicrostonyx* habitat (13.65 km², 1,365 ha) (all the habitat excluding water, mudflat, and very wet tundra) where *Dicrostonyx* would occur at the same average density as that measured on Control grids. Any overestimation of *Dicrostonyx* habitat, such as high rocky ground that might support a low density, may be balanced by underestimation of *Dicrostonyx* in wet habitats, where they were sometimes caught during the peak. Eberhardt *et al.* (1992) estimated that the dry land portion of the 20-km² home ranges they measured was 10.4 km². I assumed that on average 2 adult foxes and 4 pups used the estimated 1,365-ha area in 1995 (den F5 was only temporarily occupied, but two dens within 2 – 3 km had this litter size), and 2 adults and 11 pups in 1996 (den F5).

In 1994 and 1997 no foxes bred in the area. I saw at least 3 different individual foxes in May 1994, 2 in August 1994, and 5 in June 1997. I assumed that only 1 fox used the

estimated 1,365 ha area described above throughout summer 1994, and 2 used it throughout summer 1997.

Numerical responses of avian predators

Rough-legged hawks did not breed in the study area (see above) in 1994, but bred in 1995 (1 nest), 1996 (4 nests) and 1997 (1 nest); clutch sizes and numbers of hatchlings were generally highest in 1996 (Table 3-5). The closest nest was more than 2 km from the trapping grids and rough-legged hawks were not often seen near the grids.

Peregrine falcons and sandhill cranes did not seem to respond numerically to lemming abundance. Each year one pair of peregrines nested in the study area; in 1995 the nest failed, but chicks hatched in 1994 and 1996 and fledged in 1994 (Table 3-5; I do not have data about hatching in 1997 or fledging in 1996). The mean density of sandhill crane nests was highest in 1994 and 1996 and clutch sizes were similar among years (Table 3-5; R.G. Bromley unpublished). Both peregrines and sandhill cranes were occasionally seen near trapping grids.

Snowy owls bred in the study area only during the lemming peak (Table 3-5). There were 5 nests in the study area and at least 5 others within 7 km of the trapping grids. One nest failed (the male died or departed) but chicks hatched at 3 others (the remainder were not revisited). The known numbers of chicks per nest were 8, 7, and 4. I rarely saw snowy owls near the trapping grids except in spring and in August 1995 and 1996. In August 1995 I saw 1 – 2 owls at a time, and once 4; in August 1996 I several times saw 2 – 3 owls, and once 6. From 4 – 14 September 1996, a worker saw 6 – 10 owls in the area each day. In October 1996, owls were exceedingly common on Victoria Island to the north – an observer walking 10 km on the south shore counted about 50 (D.R. Stern, pers. comm.).

Table 3-5. a) Numbers of known nests or pairs of avian predators within the 35-km² study area that was regularly visited or searched in 1994 through 1997. Territorial pairs of pomarine jaegers were counted in an aerial search of 11.1 km² within this area (Chapter 4). I saw one territorial pair of long-tailed jaegers. Sandhill crane figures show numbers of nests found and, in parentheses, mean number per km² in 10 – 12 km² searched each year (R.G. Bromley, unpubl.).

b) Known clutch sizes (e), chicks hatched (h), and chicks fledged (fl) in the above nests.

Sandhill crane data are mean (and SE) clutch sizes (R.G. Bromley, unpubl.).

a) Nests	1994	1995	1996	1997
Rough-legged hawk		1	4	1
Peregrine falcon	1	1 (failed)	1	1
Snowy owl			5 (1 failed)	
Pomarine jaeger			17 pairs	
Long-tailed jaeger			1 pair	
Sandhill crane	9 (0.84)	6 (0.60)	10 (0.83)	4 (0.33)
b) Nesting data	1994	1995	1996	1997
Rough-legged hawk	—	4e, 3h, 3fl	6e, 4h 5e, 4h 3h, 2fl	2e
Peregrine falcon	4e, 3h, 3fl	3e, 2h, 0fl	4e, 3h	4e
Snowy owl			8e, 8h 7e, 0h 7e, 7h	
Pomarine jaeger			typically 2e	
Sandhill crane	1.6 (0.17)	2.0 (1.7)	1.9 (0.11)	1.3 (0.34)

Pomarine jaegers bred in the study area only during the lemming peak: 17 territorial pairs of pomarine jaegers were counted in an aerial search of 11.1 km² (Chapter 4; Table 3-5, this chapter). Several pairs of pomarine jaegers nested near the trapping grids. In 1996 I saw a pair of territorial long-tailed jaegers but I did not find their nest. Short-eared owls were seen in the study area in 1995 – 1997, but I found no nests.

In late August and September of the peak year, avian predators in addition to snowy owls were very abundant in migration – up to 8 short-eared owls at a time and 2 peregrine falcons perched on high points at the research camp on several occasions. Pomarine jaegers and glaucous gulls were still present in August; observers saw approximately 4 – 6 jaegers and 0 – 2 gulls daily. Flocks of migrating predatory birds stopped temporarily in the area – for example, a flock of 30 gulls was seen on 25 August 1996.

Numerical response of ermine

Ermine were rarely seen in 1994 or 1995. In June 1994, to prevent an artificial increase in the abundance of predators, I removed an ermine that was scavenging at the research camp. I saw ermine several times later in 1994. I saw one ermine in June 1995; then in July I found one apparently dead of starvation in the Exclosure, and saw none later that year. In 1996 a female raised 7 offspring on the ridge between Control grids 1 and 2; I ear-tagged 5 of these juveniles. In August 1996 several ermine were seen on trapping grids and elsewhere in the study area, but ermine killed few of our telemetered lemmings (although the fates of some lemmings were unknown); I removed two ermine from the Exclosure in 1996. One of the young females tagged in 1996 raised 4 offspring on the same ridge in 1997; I marked two. In 1997 a male ermine also used dens on and near the ridge (H. Steen, unpublished). I saw only one ermine elsewhere in 1997, an untagged animal in the predator exclosure in August.

Occupation of lemming winter nests by ermine

I found few instances of occupation by ermine of lemming winter nests in any year (maximum 4% in 1996-7, Table 3-6). I found only one nest (in 1997) clearly occupied by ermine for a long time – it contained layers of fur, ermine scats, and lemming caeca. This nest was on Control 2 grid and had probably been used by one of the two adults caught later on the ridge nearby. In 1996, one nest contained a lemming skin, and in 1997, 4 nests contained small tufts of fur; both are typical signs of ermine predation. I did not classify these nests as having been occupied by ermine, but they may indicate instances of predation after which the ermine did not stay in the nest. In each of 1996 and 1997 I found a nest containing dead juvenile lemmings, suggesting that the mother had been killed.

The factor “year” was not retained in a logistic regression model of the proportion of occupied nests as a function of year ($\Delta AIC = 1.6$). When nests with other signs of ermine predation in 1997 were also considered, year was retained in the model but the proportion of nests with signs of ermine in 1997 did not differ significantly from the proportions in the other years ($t_{294} = 0.6$, $p > 0.5$).

The number of winter nests was significantly correlated with spring lemming density on each grid (Pearson correlation coefficient $r = 0.6$, $t_{14} = 2.9$, $p < 0.02$) but not with autumn lemming density ($r = -0.1$). However, in most years the abundance of nests varied considerably among grids (Table 3-6). Mounds of lemming faeces near burrows in spring were often not associated with winter nests, suggesting that some lemmings nested underground in winter. Habitat and snow and ice conditions may affect both where lemmings nest in winter and whether they build above-ground nests or are able to use burrows. At Walker Bay, therefore, the absolute number of nests occupied by ermine may be a poor indicator of the number of lemmings killed.

Table 3-6. Numbers of winter nests examined, numbers that had been occupied by ermine, and numbers found per hectare on searched trapping grids in 1994 through 1997. In 1994 I searched three additional Control grids (Control 5, 6, and 7) on upland habitat that I neither searched nor trapped on in subsequent years. Nests with other “signs of ermine predation” contained a lemming skin (in 1996) and tufts of fur (in 1997).

Year	Counts of winter nests			Percent of nests occupied by ermine	Grid	Nests ha ⁻¹
	total found	occupied by ermine	signs of ermine predation			
1994	45	1	0	2%	Control 2	1.3
					Control 3	1.3
					Control 5	1.8
					Control 6	1.4
					Control 7	0.5
1995	66	0	0	0%	Control 1	1.6
					Control 2	2.8
1996	110	1	1	1%	Control 1	6.4
					Control 2	0.8
					Control 3	2.4
					Exclosure	5.2
1997	77	3	4	4%	Control 1	2.1
					Control 2	2.1
					Control 3	2.2

Discrimination of adult and juvenile fox scats

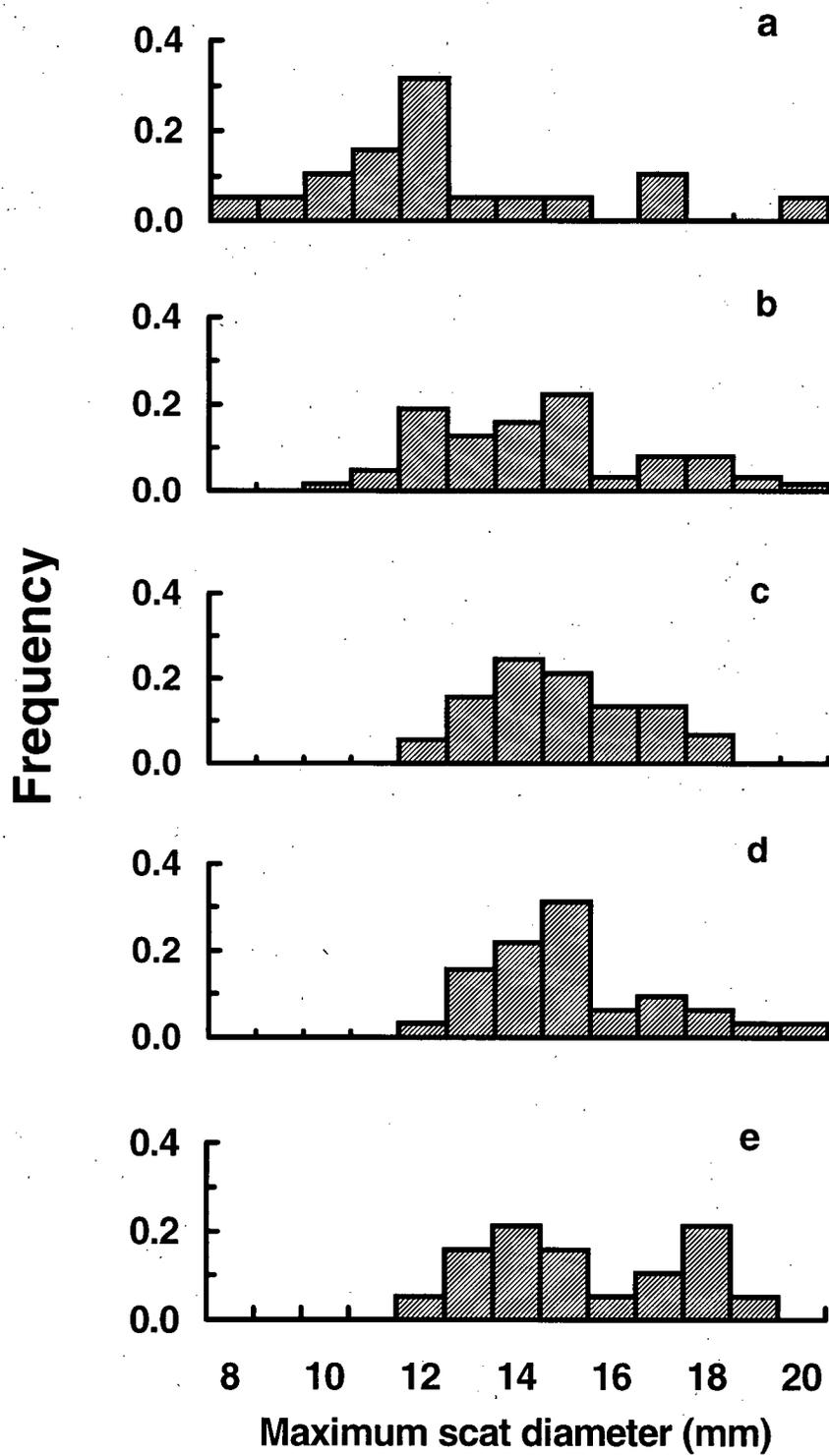
There was a shift in the distribution of the diameters of scats collected from dens as summer 1996 progressed (Fig. 3-2). The diameters of scats from dens in June and July had a somewhat bimodal distribution, with many scats of diameter ≤ 12 mm, whereas few such small scats were collected from dens later in summer or opportunistically (not from active dens) throughout summer. Therefore I assumed that all scats of diameter ≤ 12 mm collected at active natal dens in June and July 1995 and 1996 were those of juvenile foxes.

Occurrence of prey types in scats

Lemming remains, most often *Dicrostonyx*, were found in most scats, in both summer and winter (Table 3-7). Ground squirrel, bird and insect remains often occurred in adult fox scats. Eggshell was found in adult fox scats collected in June 1995 and 1996 and in scats from the preceding winters, suggesting that foxes retrieved eggs cached during the previous spring. No eggshells were found in scats in 1997, a year when few geese nested (Chapter 4). Insects, caribou (*Rangifer tarandus*), arctic hare (*Lepus arcticus*), arctic fox, and shrews (*Sorex ugyunak* Anderson and Rand) were less common prey items in adult fox scats. One scat found early in 1996 contained white fox hair and little else; I assumed the hair was from grooming during the moulting period and omitted this scat from estimates of biomass consumption. A few scats contained a large amount of vegetation.

Scats from juvenile foxes (Table 3-7b) contained a smaller variety of remains than did adult scats. Lemmings occurred in 95% (n = 19) of juvenile scats in 1995 and in 100% (n = 21) in 1996. In 1995 some juvenile scats contained squirrel and bird remains but in 1996 the only prey items in juvenile scats were lemmings. No juvenile scats contained eggshell.

Fig. 3-2. Frequency distributions of the diameters of arctic fox scats collected from active dens in 1996 during the sampling periods (a) 1 June – 3 July, (b) 7 – 21 July, (c) 30 July – 8 August, (d) 17 – 28 August; and (e) scats collected opportunistically (not from active fox dens) throughout the summer of 1996.



b) Scats of juvenile arctic foxes

N	1995		1996	
	15 Jun-	1 Jun-	1 Jul	7-21 Jul
	2 Aug	1 Jul	6	15
Lemming	95	100	100	100
<i>Dicrostonyx</i>	68	100	100	87
<i>Lemmus</i>	16	0	0	33
Unknown sp.	16	0	0	0
Squirrel	16	0	0	0
Hare	0	0	0	0
Fox	0	0	0	0
Shrew	0	0	0	0
Caribou	0	0	0	0
Birds				
Large	5	0	0	0
Small	11	0	0	0
Eggshell	0	0	0	0
Invertebrate	0	0	0	0
Unidentified	11	0	0	0

Biomass of prey remains in arctic fox scats

The mean estimated biomass of all ingested animal material per adult fox scat, based on biomass in scats and conversion factors for different prey (Appendix 1), exceeded 50 g in most sampling periods (Table 3-8a). Exceptions were the winters of 1994-5 (mean 40.2 g, n = 6) and 1995-6 (40.2 g, n = 20), early in the summer of 1995 (37.3 g, n = 20), and late in 1997 (15.9 g, n = 3). Food may have been relatively scarce during these periods. In July 1996 the mean biomass per scat was quite low (45.2, n = 24) even though lemmings were plentiful; some juvenile fox scats may have been mixed in my sample of adult scats.

Lemmings accounted for 44 – 100% of the total biomass in each sampling period. In scats in which the species of lemming remains could be identified, *Dicrostonyx* accounted for 42 – 88% and *Lemmus* for 0 – 28%. Because the estimation of total ingested biomass was very approximate (Appendix 1), I have not based further conclusions or statistical comparisons on these estimates.

Scats from juvenile foxes accounted for less ingested biomass than did scats from adults (Table 3-8b). In June 1996 biomass in juvenile scats represented on average 22.8 g of ingested biomass; in July 1995 and 1996 juvenile scats represented approximately 35 g. Lemmings accounted for 71% of the biomass ingested by juvenile foxes in 1995 and 100% in 1996. As with adult foxes, most of the identifiable lemming remains were *Dicrostonyx*.

Daily consumption of *Dicrostonyx* biomass

For the purpose of estimating the defecation rate of foxes, I considered that foxes (adults and juveniles) were well fed only during summer 1996 (5 scats day⁻¹). At other times there were indications of food shortage: foxes did not breed in 1994 and 1997, and in 1995 one pup died, one litter apparently failed (Table 3-4), and juveniles and adults at dens seemed lethargic. The biomass per scat was also low during these periods (Table 3-8). Because biomass per scat was

Table 3-8. Mean biomass (g) ingested per (a) adult fox scat and (b) juvenile fox scat. Total animal biomass, lemming biomass, and the percentage of the total represented by lemming, are given. For scats in which the species of lemming could be determined, biomass and percent of total biomass are given for *Dicrostonyx* and *Lemmus*.

	1994		1994-5		1995		1995-6		1996		1996-7		1997	
	summer	winter	16 Jun-14 Jul	15 Jul-2 Aug	22-25 Aug	winter	1 Jun-1 Jul	7-21 Jul	30 Jul-8 Aug	14-21 Aug	winter	7 Jun-7 Jul	4-18 Aug	3
<u>All scats</u>														
N	10	6	20	21	19	20	11	24	30	20	13	13	13	3
Animal biomass	51.0	40.2	37.6	46.9	69.8	40.2	65.1	45.2	65.7	62.7	56.7	51.4	51.4	15.9
1 SE	11.3	6.3	6.6	6.2	10.8	6.4	8.2	5.5	5.3	11.5	9.3	7.7	7.7	2.7
Lemming	33.0	25.6	20.6	37.9	30.4	35.8	62.0	40.0	56.9	52.5	56.4	49.5	49.5	13.8
1 SE	11.5	11.1	4.4	5.5	6.0	5.6	7.3	5.5	5.2	6.0	9.3	7.6	7.6	1.4
% of total biomass	65	64	55	81	44	89	95	88	87	84	100	96	96	87
<u>Scats in which lemming species could be identified</u>														
N	9	5	20	19	15	20	11	23	28	18	12	13	13	3
Animal biomass	52.6	41.2	37.6	50.0	59.8	40.2	65.1	42.9	65.2	54.5	57.8	51.4	51.4	15.9
1 SE	12.5	7.6	6.6	6.3	12.2	6.4	8.2	5.2	5.5	6.4	10.1	7.7	7.7	2.7
<i>Dicrostonyx</i>	23.5	30.7	17.4	35.4	25.2	30.2	55.8	31.7	54.8	47.8	41.1	37.7	37.7	13.8
1 SE	9.9	12.1	4.4	6.4	6.5	6.1	5.7	5.0	5.7	7.1	12.2	9.1	9.1	1.4
% of total biomass	45	75	46	71	42	75	86	74	84	88	71	73	73	87
<i>Lemmus</i>	11.0	0.0	3.2	5.8	3.9	5.5	6.2	9.9	4.4	5.8	16.5	11.7	11.7	0.0
1 SE	7.9	0.0	2.6	2.8	2.7	3.4	4.2	5.5	2.1	3.7	8.6	6.5	6.5	0.0
% of total biomass	21	0	8	12	7	14	9	23	7	11	28	23	23	0

b) Scats of juvenile arctic foxes

	1995		1996	
	15 Jun- 2 Aug		1 Jun- 1 Jul	7-21 Jul
<u>All scats</u>				
N	19		6	15
Animal biomass	34.4		22.8	35.8
1 SE	3.5		4.6	3.9
Lemming	24.6		22.8	35.8
1 SE	3.0		4.6	3.9
% of total biomass	71		100	100
<u>Scats in which lemming species could be identified</u>				
N	16		6	15
Animal biomass	35.4		22.8	35.8
1 SE	3.9		4.6	3.9
<i>Dicrostonyx</i>	21.7		22.8	28.1
1 SE	3.9		4.6	4.7
% of total biomass	61		100	78
<i>Lemmus</i>	3.9		0.0	7.7
1 SE	2.1		0.0	3.3
% of total biomass	11		0	22

very low in August 1997, I assumed severe food stress during this period (3 scats day⁻¹), and moderate food stress throughout 1994, 1995, June 1997, and all three winters (4 scats day⁻¹).

Juvenile arctic foxes are born in May or June, emerge from the den after 3 – 4 weeks, and are weaned at 6 – 7 weeks of age (Garrott and Eberhardt 1987). I first saw juveniles at dens on 28 July 1995 and 25 June 1996. I assumed that juveniles from 16 June – 14 July 1995 and 1 June – 1 July 1996 had half the defecation rate of adults because they were not fully weaned (Reid *et al.* 1997 made the same assumption). I considered that pups were equivalent to adults in August, when they were hunting independently and their scats could no longer be distinguished.

Functional response of arctic foxes: number of individual lemmings consumed

The ratios of adult (> 40 g) to juvenile (\leq 40 g) lemmings in scats ranged from 1:6 to 5:8 in the 4 summer periods of 1996 and during 7 June – 7 July 1997 (Table 3-9). These were the only sampling periods when I could determine the size of at least 4 lemmings from their remains. During the same periods the corresponding ratios of adults to juveniles caught in live-traps ranged from 1.8:1 to 4:1. The fact that the proportion of adults in scats was much lower than the proportion trapped suggests that juveniles were more susceptible to fox predation than were adults. The average correction factor indicating the reduced vulnerability of adults relative to juveniles (proportion in scats \div proportion caught) was 0.18 (Table 3-9). The adjusted ratios of adult to juvenile lemmings killed by foxes in all sampling periods, estimated by multiplying the ratios of adults to juveniles trapped in each sampling period by this correction factor, are shown in Table 3-10. Applying these ratios and the mean mass of adult and juvenile lemmings caught in each period to the estimated daily biomass of *Dicrostonyx* consumed per fox yielded estimates of up to 6.9 *Dicrostonyx* consumed daily per adult fox and up to 3.3 per juvenile fox (Table 3-10). When *Lemmus* were included the corresponding estimates of daily lemming consumption were 7.4 and 4.3 individuals.

Table 3-9. Estimation of ratio of adult to subadult lemmings killed by foxes.

	1996				1997
	1 Jun- 1 Jul	7-21 Jul	30 Jul- 8 Aug	14-21 Aug	7 Jun- 7 Jul
Adult:juvenile lemmings in scats	2:4	1:6	5:8	2:6	1:3
(1) Convert to fraction: Adults/juveniles	0.50	0.17	0.63	0.33	0.33
(2) Adult/juvenile lemmings trapped	3.97	2.78	1.82	2.20	1.71
(1) / (2) Vulnerability of adults relative to juveniles	0.13	0.06	0.34	0.15	0.20
(3) Mean relative vulnerability: 0.18					
(2) x (3) Adjusted adult/juvenile lemmings killed	0.70	0.49	0.32	0.39	0.30

Table 3-10. Estimation of daily consumption of *Dicrostonyx* by arctic foxes in 1994 – 1997, based on biomass in scats, estimated defecation rates, known numbers of arctic foxes in breeding summers (1995-6) and estimated numbers of foxes in other periods.

	1994		1994-5		1995		1995-6		1996		1996-7		1997	
	summer	winter	16 Jun-14 Jul	15 Jul-2 Aug	2 Aug	15 Jul-2 Aug	22-25 Aug	winter	1 Jun-1 Jul	7-21 Jul	30 Jul-8 Aug	14-21 Aug	winter	7 Jun-4 Aug
<i>Dicrostonyx</i> (g scat ⁻¹)														
Adult foxes	23.5	30.7	17.4	35.4	25.2	30.2	55.8	31.7	54.8	47.8	41.1	37.7	13.8	
Juvenile foxes				21.7			22.8	28.1						
Defecation rate (scats day ⁻¹)														
Adult foxes	4	4	4	4	4	4	5	5	5	5	4	4	4	3
Juvenile foxes ^a			2	4			2.5	5						
<i>Dicrostonyx</i> (g day ⁻¹ fox ⁻¹)														
Adult foxes	94	123	70	142	101	121	279	158	274	239	164	151	41	
Juvenile foxes ^b			35	87			57	141						
Adult/juvenile lemmings trapped ^c	1.00	2.00	16.00	1.43	2.33	2.00	3.97	2.78	1.82	2.20	100	1.71	2.62	
Correction factor ^d	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18	0.18
Estimated adult/juvenile lemmings killed	0.18	0.35	2.81	0.25	0.41	0.35	0.70	0.49	0.32	0.39	17.53	0.30	0.46	
<i>Dicrostonyx</i> live mass ^e (g)														
Adults (>40 g)	64.3	64.3	67.8	67.9	58.9	64.3	67.7	70.7	63.4	58.2	64.3	57.3	58.6	
1 SE	0.6	0.6	3.4	3.7	3.1	0.6	1.6	1.5	1.5	1.3	0.6	1.2	2.1	
Juveniles (<=40 g)	31.9	31.9	40.4	33.0	32.6	31.9	30.8	29.6	32.3	34.6	31.9	29.7	28.5	
1 SE	0.4	0.4	--	0.0	1.8	0.4	1.3	1.0	0.8	0.7	0.4	1.0	2.3	

Table 3-10, continued.

	1994		1994-5		1995		1995-6		1996		1996-7		1997	
	summer	winter	16 Jun- 14 Jul	15 Jul- 2 Aug	22-25 Aug	winter	1 Jun- 1 Jul	7-21 Jul	30 Jul- 8 Aug	14-21 Aug	winter	7 Jun- 7 Jul	4-18 Aug	
<i>Dicrostonyx</i> eaten (no. day ⁻¹ fox ⁻¹)														
Adult foxes	2.6	3.0	1.1	3.5	2.5	3.0	6.1	3.7	6.9	5.8	2.6	4.2	1.1	
Adult lemmings	0.4	0.8	0.8	0.7	0.7	0.8	2.5	1.2	1.7	1.6	2.5	1.0	0.3	
Juvenile lemmings	2.2	2.3	0.3	2.8	1.8	2.2	3.6	2.5	5.2	4.2	0.1	3.2	0.7	
Juvenile foxes			0.6	2.2			1.2	3.3						
Adult lemmings			0.4	0.4			0.5	1.1						
Juvenile lemmings			0.2	1.7			0.7	2.2						
Number of foxes														
Adults	1	1	2	2	6	3	2	2	13	13	7	2	2	
Juveniles			4	4			11	11						
Total <i>Dicrostonyx</i> eaten day ⁻¹														
Adult lemmings	0.4	0.8	3.4	3.2	4.4	2.3	10.6	14.2	21.6	21.0	17.4	1.9	0.7	
Juvenile lemmings	2.2	2.3	1.2	12.6	10.7	6.7	15.2	29.1	67.9	54.4	1.0	6.4	1.5	

^a I halved the number of juvenile scats in June because juveniles are not weaned until approximately the end of June

^b I assumed the biomass of *Dicrostonyx* juvenile scats in the first period of 1995 was the same as that in adult scats during the same period

^c Estimates for winter: 2 for 1994-5 and 1995-6; 100 for 1996-7 assuming low winter reproduction after the peak summer.

^d Correction factor from Table 3-9 for reduced vulnerability of adult lemmings relative to juveniles.

^e Winter and 1994 mass is average of mass in all other sampling periods.

The plot of numbers of individual *Dicrostonyx* consumed per fox as a function of prey density (Fig. 3-3) suggests a Type II functional response (Holling 1959a), but the curve-fitting algorithm could not solve equation (1) unless the high consumption at very low density in 1994 was deleted. Without this datum, the curve fitted to the adult fox data had $m = 0.26$, indicating no evidence of a Type III response (sigmoid curves have $m > 1$). A Type II curve appears more strongly indicated with the low-density datum present, but this high consumption may be a result of my mistaking old scats, from previous years when lemming density was higher, for fresh ones. The apparent lack of an asymptote was dependent on my assumption of different defecation rates at different lemming densities; with a constant defecation rate of 4 scats day⁻¹, the best value was $m = 0.7$. In short, there was no evidence of a Type III response, although without more scats from low lemming densities it is best to be cautious about this conclusion. As mentioned above, the low daily consumption by adults in June 1996, which was very similar to that of juvenile foxes, may be a result of accidentally including juvenile scats in the sample of adult scats.

Predation rate estimated from fox scats

The product of the number of lemmings eaten per fox and the estimated number of foxes in the 25 km² area equals the estimated number of *Dicrostonyx* killed daily in the area (Table 3-10). The rates of predation by arctic foxes in 14 days, estimated by converting these values to units of ha⁻¹ 14 days⁻¹ and dividing by mean *Dicrostonyx* density on Control grids during each sampling period, were remarkably similar to those determined from radio-telemetry (Table 3-11) in 1996 and early in 1997. Rates of fox predation per 14 days estimated from telemetry in these sampling periods varied from about 0.032 in June 1997 to 0.079 in July 1996; rates estimated from fox scats varied from 0.035 to 0.064. The correspondence was weaker in 1995 and poor late in 1997; in these periods sample sizes for radio-telemetry were low (Chapter 2). In August 1997 there were several additional sources of error – only 3 scats were collected, population

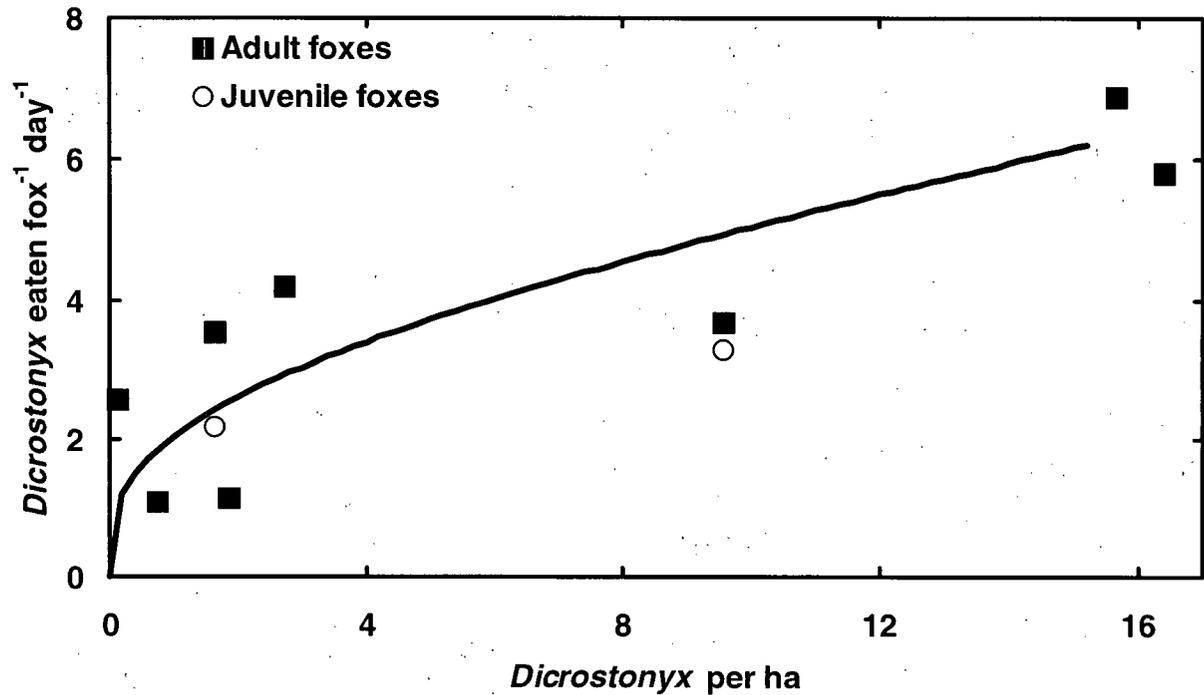


Fig. 3-3. Functional responses of adult (filled squares) and juvenile (open circles) arctic foxes to lemming density, which was estimated by means of mark-recapture (Chapter 2). Lemming densities are the means of estimates on Control grids (not protected from predators). In the period 7 June – 7 July 1997, density is the mean of estimates on Control grids from 15-18 June and 28 June – 5 July. The high daily consumption in 1994 may be a result of my mistaking old scats for fresh ones. The low daily consumption by adults in June 1996 may be a result of confusing juvenile with adult scats. The curve fitted to the adult fox data, without the 1994 datum, has the form of equation (1), where $m = 0.26$.

Table 3-11. Estimation of mortality rates of *Dicrostonyx* from fox scats (see Table 3-10), compared to mortality rates estimated from radio-telemetry data.

	1994		1994-5		1995		1995-6		1996		1996-7		1997	
	summer	winter	16 Jun-14 Jul	16 Jun-14 Jul	15 Jul-2 Aug	15 Jul-2 Aug	22-25 Aug	1 Jun-1 Jul	7-21 Jul	30 Jul-8 Aug	14-21 Aug	winter	7 Jun-7 Jul	4-18 Aug
Consumption by arctic foxes														
<i>Dicrostonyx</i> eaten d^{-1}	2.6	3.0	4.6	4.6	15.7	15.1	15.1	9.0	25.8	43.3	89.5	18.4	8.4	2.2
<i>Dicrostonyx</i> $14 d^{-1} ha^{-1}$	0.026	0.031	0.047	0.047	0.162	0.154	0.092	0.265	0.444	0.918	0.774	0.189	0.086	0.022
Density of <i>Dicrostonyx</i> (ha^{-1})	0.11		1.86	1.65					9.59	15.65	16.42		2.72	0.74
Mortality rate from fox scats ($14 d^{-1}$)	0.239		0.025	0.098					0.046	0.059	0.047		0.032	0.030
Mortality rates from radio-telemetry														
Fox predation only ($14 d^{-1}$)			0.057	0	0.036			0.028	0.079	0.060	0.060		0.032	0.192
Overall mortality ($14 d^{-1}$)			0.131	0.125	0.036		0.089	0.090	0.060	0.060	0.060		0.060	0.285

density was declining, and it was difficult to estimate the number of foxes using the area. Estimated rates of fox predation were high only in 1994 (0.24, estimated from scats) and in August 1997 (0.19, estimated from ratio-telemetry).

Prey remains in pellets from avian predators

Lemming remains occurred in all pellets of rough-legged hawks in 1995 – 1997, short-eared owls in 1995, snowy owls in 1994 – 1997, and pomarine jaegers and a sandhill crane (n = 1) in 1996 (Table 3-12). No pellets from peregrine falcons contained lemming remains in 1994, but lemming was found in 25 – 60% of these pellets in 1995 – 1997. All glaucous gull pellets contained lemming remains in 1996 (n = 11) but did not in 1994 (n = 1) or 1995 (n = 1).

Dicrostonyx was the sole lemming species in pellets of pomarine jaegers, peregrine falcons, and the sandhill crane; all other species of avian predators had consumed both species of lemmings, *Dicrostonyx* more often than *Lemmus*.

All the birds of prey ate small birds and insects in addition to lemmings, except that the single sandhill crane pellet contained lemming remains only. Eggshell was found in one rough-legged hawk pellet, one peregrine falcon pellet, and four gull pellets. Arctic ground squirrel remains were found in two rough-legged hawk pellets and one peregrine falcon pellet. Mollusc shell was found in both glaucous gull pellets from 1994 and 1995. In 1995, one rough-legged hawk pellet contained remains of five tundra voles (*Microtus oeconomus*), which I never trapped at Walker Bay. Two short-eared owl pellets in 1995 each had remains of two shrews. Two fox scats also contained shrew remains in 1995 (Table 3-12a), and I caught more shrews in lemming traps in 1995 than in other years.

Individual short-eared owl and pomarine jaeger pellets had a maximum of two lemmings, glaucous gull pellets from one to four, and peregrine falcon pellets a maximum of one lemming (Fig. 3-4). Rough-legged hawk pellets contained from one to four lemmings (one *Dicrostonyx*

Table 3-12. Frequency of occurrence of different prey items in pellets of rough-legged hawks, short-eared owls, snowy owls, peregrine falcons, pomarine jaegers, glaucous gulls, and a sandhill crane pellet.

% Frequency of occurrence	Short-eared			Snowy owl				Pomarine			Sandhill						
	Rough-legged hawk		owl	1994 1995 1996 1996-7 1997				jaeger			crane						
	1995	1996	1997	1994	1995	1996	1996-7	1994	1995	1996	1994	1995	1996				
N	12	20	1	1	3	31	9	4	16	16	8	5	24	1	1	11	1
Lenming	100	100	100	100	100	100	100	100	0	31	25	60	100	0	0	100	100
<i>Dicrostonyx</i>	92	95	100	100	100	100	89	100	0	31	25	60	100	0	0	64	100
<i>Lemmus</i>	17	15	0	33	0	33	19	56	75	0	0	0	0	0	0	36	0
<i>Microtus</i> vole	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Squirrel	8	5	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0
Shrew	0	0	0	33	0	0	0	0	0	0	0	0	0	0	0	0	0
Bird	33	15	100	17	100	33	13	11	50	100	100	88	100	8	100	100	9
Eggshell	0	5	0	0	0	0	0	0	0	0	0	13	0	0	0	100	27
Insect	25	0	0	0	0	0	3	0	0	0	6	0	20	13	0	100	0
Mollusc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	100	0

winter spring

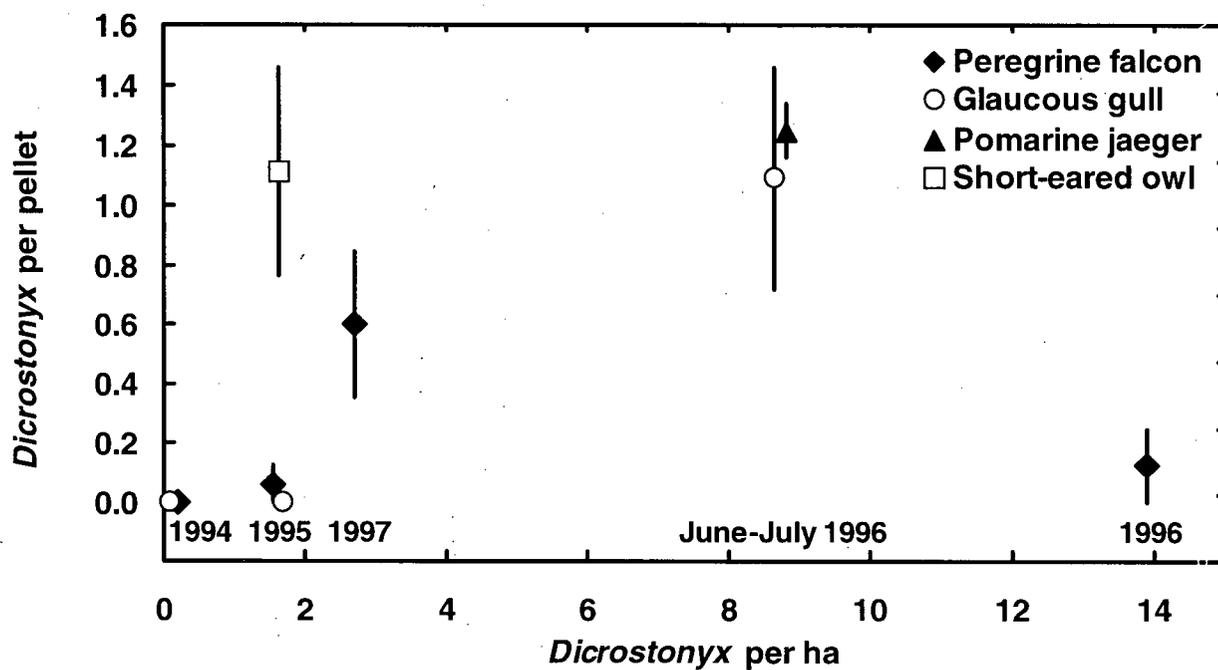


Fig. 3-4. Number of *Dicrostonyx*, indicated by unique molar teeth, found per pellet of peregrine falcons, glaucous gulls, pomarine jaegers, and short-eared owls, at different prey densities in different sampling periods.

was also in the pellet with five voles), and snowy owl pellets contained from one to eight lemmings.

Functional responses of avian predators

Since rough-legged hawks bred in each year from which I have pellets (1995 – 1997), I have no strong evidence that they were food-stressed, although clutch sizes were generally higher in the peak year (Table 3-5b). Therefore I converted the number of lemmings per pellet to lemmings ingested per day (Fig. 3-5) with the digestion factor and casting rate from Reid *et al.* (1997) for a well-fed hawk (Appendix 2). For snowy owls I used a casting rate of 1.55 pellets day⁻¹, the higher of Lockie's (1955) two estimates for short-eared owls; I chose the higher rate because most of my owl pellets came from periods when lemming density was relatively high. Daily pellet formation by owls varies with diet and among owl species; some owls may produce as many as 4 pellets day⁻¹ (reviewed by Chitty 1938). Nestling snowy owls ejected between 0.7 and 1.7 pellets day⁻¹, higher numbers as they grew larger (Watson 1957). I have no evidence of food stress in snowy owls except for the single owl seen in 1994, which left a small pellet (2 g, whereas most exceeded 10 g) containing the remains of a single lemming. For this owl I assumed a casting rate of 1 pellet day⁻¹. The casting rate of 1.55 pellets day⁻¹ yielded an estimated daily consumption of lemmings by snowy owls of 4.7 to 5 in 1995, 1996, and the winter of 1996-7, and 7 in June 1997 (Fig. 3-5).

Reproductive condition – male lemmings

A smaller proportion of large male lemmings (≥ 50 g) was reproductive in 1996 than in either 1995 ($t_{241} = 2.4$, $p < 0.02$) or 1997 ($t_{241} = 3.3$, $p < 0.001$) (Fig. 3-6a). The proportion of reproductive males was lower in August than in each preceding sampling period (June, June-July, and July-August, $t_{241} > 3.2$, $p < 0.002$). Neither trapping grid nor any interactions were

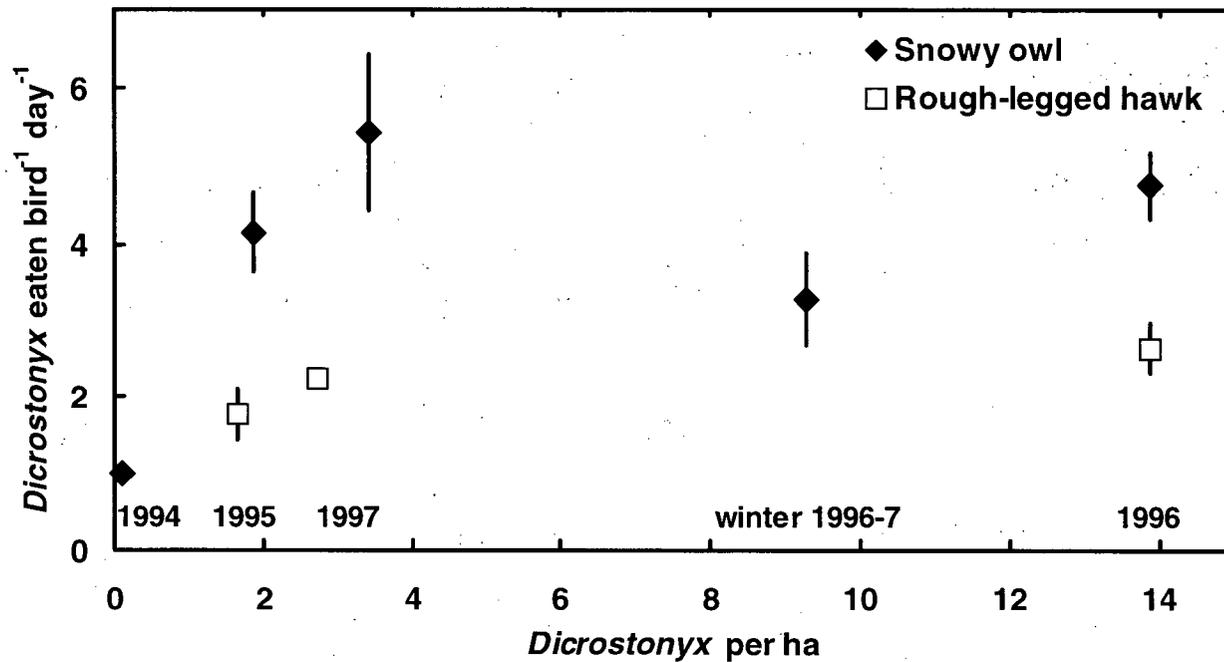
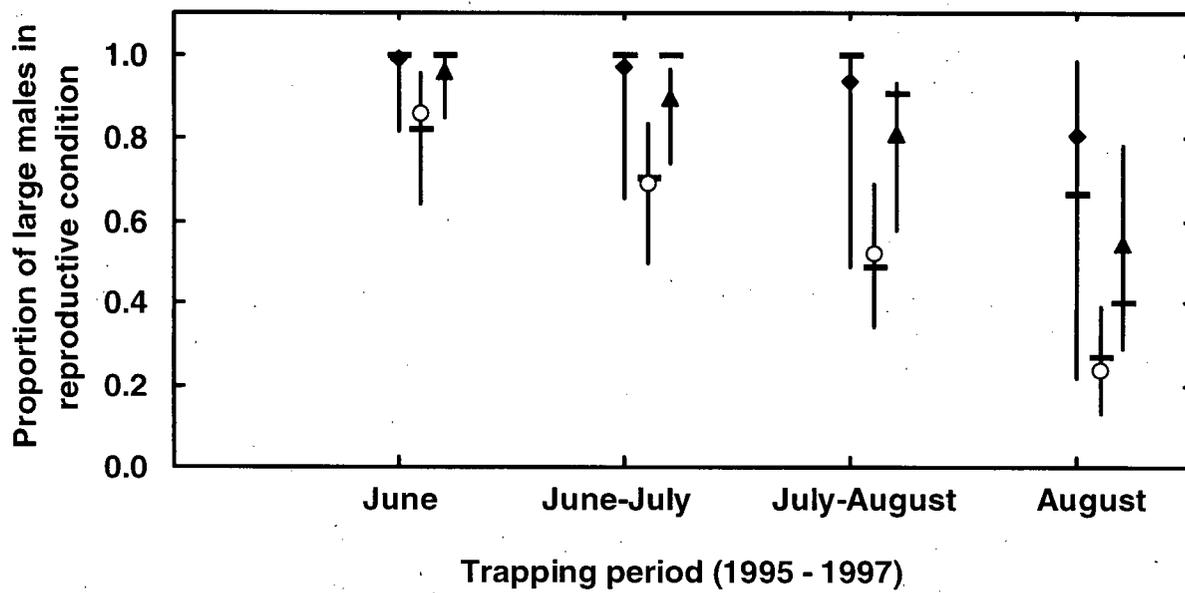


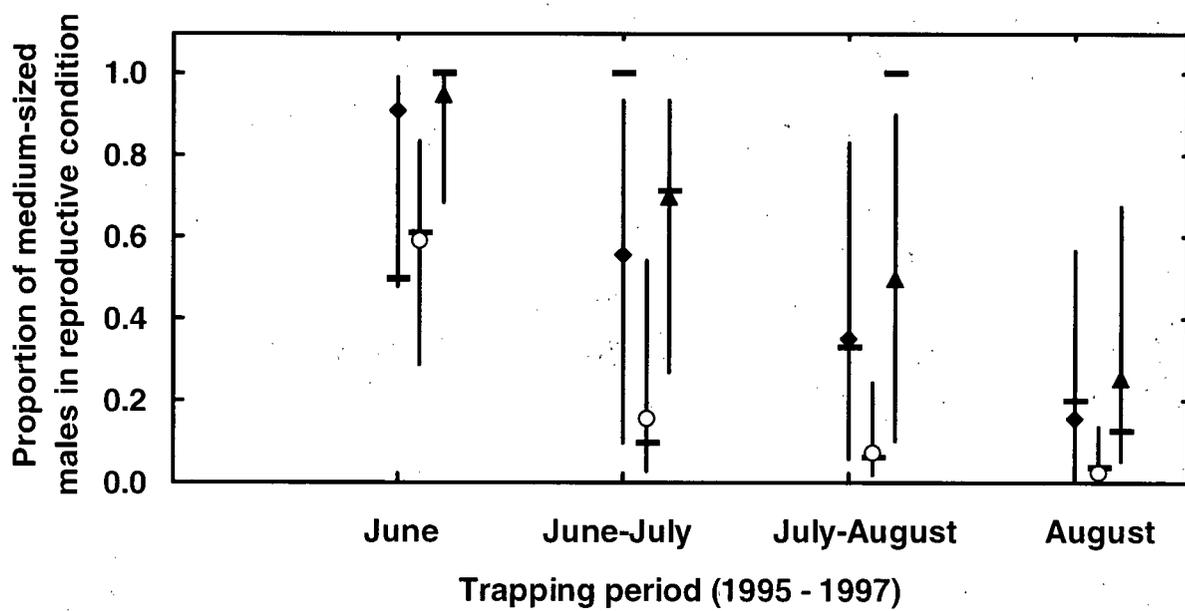
Fig. 3-5. Functional responses of snowy owls (filled diamonds) and rough-legged hawks (open squares) to density of *Dicrostonyx*, based on mean numbers of prey per pellet, estimated conversion factors for digestion in the case of hawks, and estimated daily casting rates. Error bars indicate standard errors, which were calculated based on mean numbers of prey per pellet and then multiplied by the same constants as were the means.

Fig. 3-6. The proportions of (a) large (≥ 50 g) and (b) medium-sized (25 – 49 g) male *Dicrostonyx*, caught in live-traps, that were in reproductive condition in 1995 (diamonds), 1996 (open circles), and 1997 (triangles). Points show the proportions of animals in reproductive condition, estimated by logistic regression models. Error bars represent 95% confidence intervals. Horizontal lines show the actual proportions of males in reproductive condition captured during each time period.

a)



b)



retained in the model. The actual percentage of large males that were in reproductive condition declined from 100%, 82%, and 100% in June 1995, 1996, and 1997, to 67%, 27%, and 40% in August of the three years respectively (Fig. 3-6a).

The reproductive condition of medium-sized males (25 – 49 g) followed the same pattern as that of large males (Fig. 3-6b) although a smaller proportion tended to be in reproductive condition. The fractions in reproductive condition declined from 50% ($n = 2$), 60%, and 100% in June 1995, 1996, and 1997 respectively, to 20%, 4%, and 13% in August of the same years. The differences between 1996 and the other years were significant ($t_{161} > 2.5$, $p < 0.02$). Few small males (< 25 g) were in reproductive condition (0 of 0 in 1995, 1 of 14 in 1996 and 2 of 4 in 1997). Because of the small sample size, year was the only factor tested in the model; the increase in proportion in 1997 compared with 1995 and 1996 approached statistical significance ($t_{16} = 1.79$, $p < 0.10$).

In snap-trapping surveys in June 1996 and 1997 and July 1995 and 1997, the percentage of males producing sperm (epididymis visible) varied from 50% to 100% ($n = 1$ to 8, Table 3-13). In July 1996 none of the 14 males caught were producing sperm. Only 3 of these were large males (≥ 50 g), 4 weighed 25 – 49 g, and 7 weighed < 25 g.

Reproductive condition – female lemmings

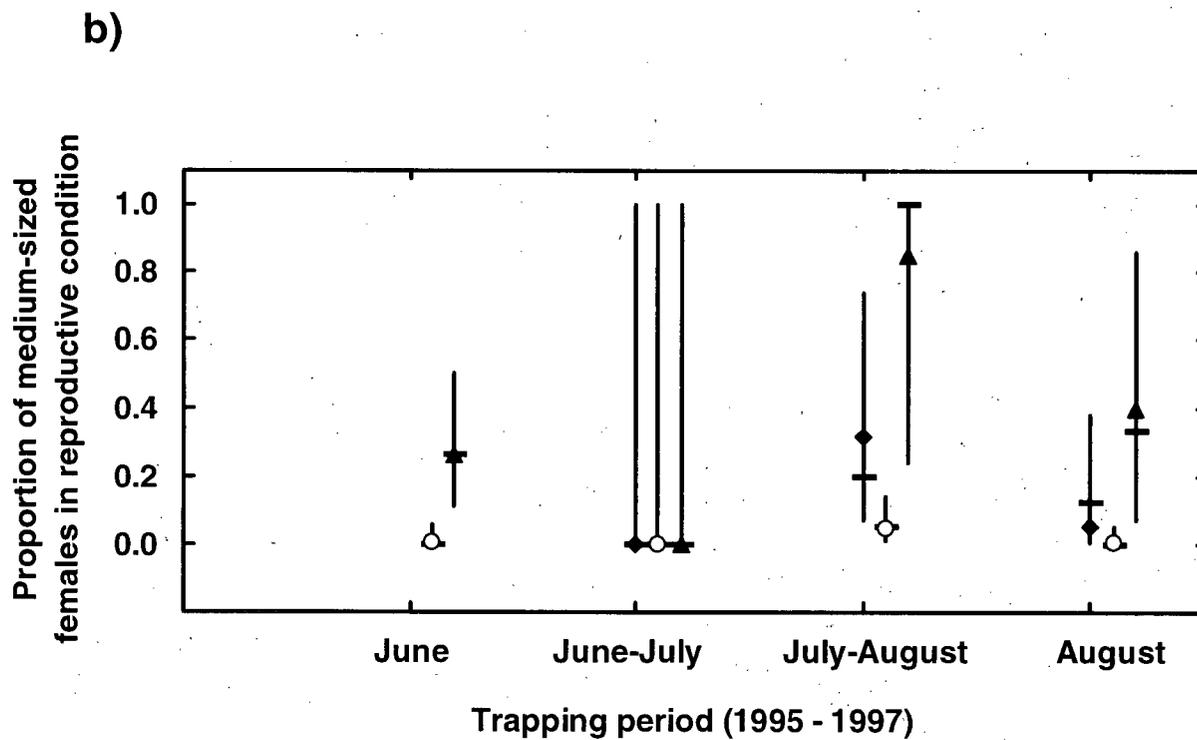
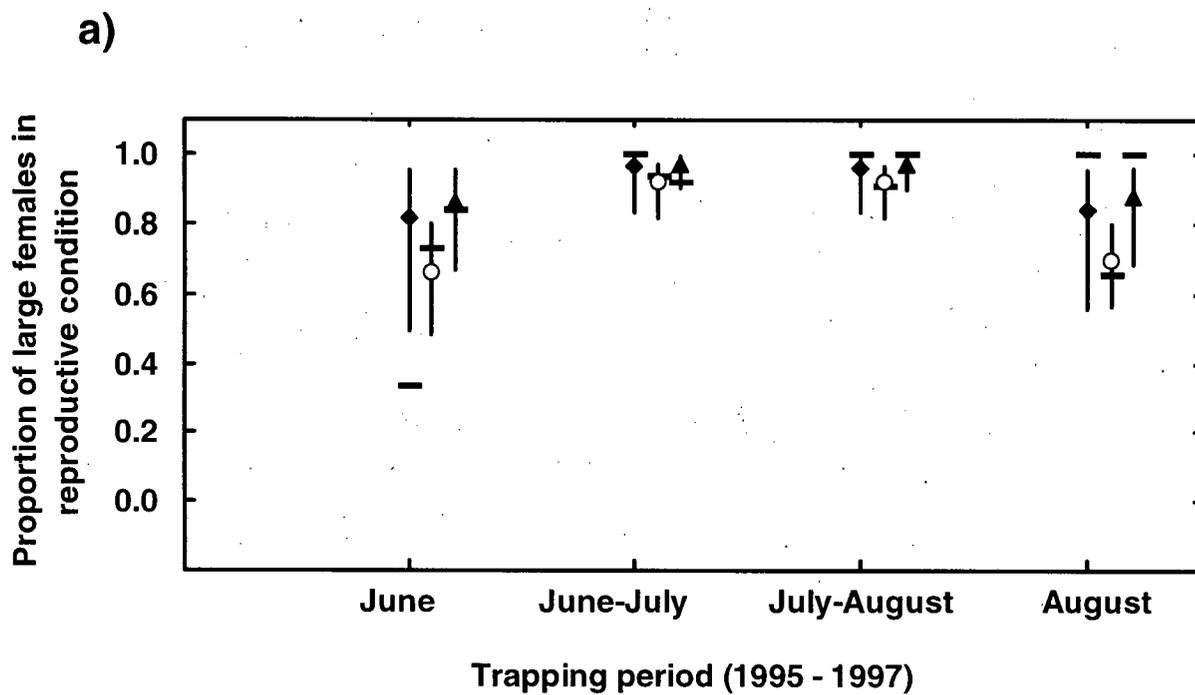
The indicators of reproductive condition of a live female, a slightly open pubic symphysis and evidence of lactation, both lag behind actual pregnancy. Most large females were in reproductive condition (Fig. 3-7a). In the model of reproductive condition of large females all terms were retained, including trapping grid ($\Delta AIC_c = -1.9$) and an interaction between year and period ($\Delta AIC_c = -0.9$). The slight interaction was evident (Fig. 3-7a) in that the actual proportion reproductive remained at 1.0 beginning in late June-July 1995 and 1997, but declined in late summer 1996. However, differences among trapping grids were neither significant nor

Table 3-13. Mass and reproductive condition of male *Dicrostonyx* caught in snap-traps at Walker Bay in June 1996 – 1997 and July 1995 – 1997. I assumed that spermatogenesis was indicated if the epididymis was visible. The reproductive status of one male was unknown because the carcass had been partly consumed by a predator.

Male *Dicrostonyx*

Year	Trapping dates	N	%			Epididymis visible	
			<25 g	25 - 50 g	>=50g	% visible	% unknown
1996	12 - 17 June	8	0	38	50	75	4
1997	17 - 23 June	2	0	50	50	50	
1995	10 - 16 July	3	0	33	67	67	
1996	11 - 16 July	14	50	29	21	0	
1997	15 - 16 July	1	0	100	0	100	

Fig. 3-7. The proportions of (a) large (≥ 50 g) and (b) medium-sized (25 – 49 g) female *Dicrostonyx*, caught in live-traps, that were in reproductive condition in 1995 (diamonds), 1996 (open circles), and 1997 (triangles). Reproductive condition did not include oestrus (see text and Fig. 3-8). Points show the proportions of animals in reproductive condition, estimated by logistic regression models. Error bars represent 95% confidence intervals. Horizontal lines in show the actual proportions of females in reproductive condition captured during each time period in each year.



consistent among sampling periods ($t_{426} = 1.2$, $p > 0.2$), and none of the interaction coefficients differed significantly from zero ($p > 0.5$). Therefore, to obtain power for comparison among years, I dropped these terms from the model. This reduced model fitted well (Fig. 3-7a) except for discrepancies resulting from deleting the interaction term: in June 1995 when the sample size was very small ($n = 6$), and in August 1995 and 1997, when although all large females were reproductive, the model estimated a smaller fraction. The conclusions drawn from this simplified model made sense when compared with the observed data (Fig. 3-7a).

A smaller proportion of large females was reproductive in 1997 than in 1996 ($t_{434} = 2.6$, $p < 0.01$). The same pattern was apparent between 1995 and 1996, but the difference was not statistically significant ($t_{434} = 1.5$, $p > 0.1$). A significantly smaller proportion of large females was reproductive in August than in June-July or in July-August ($t_{434} > 3.8$, $p < 0.0002$), and it is apparent from Fig. 3-7a that this difference was due to a decline in reproductive condition in 1996 only. All large females were reproductive in July-August and August 1995 and 1997 ($11 \leq n \leq 21$ in each period), but only 91% in July-August 1996 and 66% in August 1996 ($n > 90$).

Few medium-sized adult females were in reproductive condition (Fig. 3-7b) but the proportion of medium-sized females that were reproductive was greater in both 1995 ($t_{183} = 2.6$, $p < 0.02$) and 1997 ($t_{183} = 3.1$, $p < 0.005$) than in 1996. The fraction of reproductive medium-sized females trapped in 1996 never exceeded 5% ($4 \leq n \leq 61$ in each period), but was 12.5% in August 1995 ($n = 8$), 28% in June 1997 ($n = 8$), and 33% in August 1997 ($n = 3$). The only time period in which the proportion of reproductive females approached a significantly higher level than that in August was the July-August time period ($t_{183} = 1.95$, $p < 0.06$). There were no significant differences among trapping grids ($p > 0.1$, Chapter 2). No small females were classified as reproductive.

I could not compare the absolute proportions of females in oestrus among years because of differences in assessments among field workers, but I estimated the change in rates of oestrus

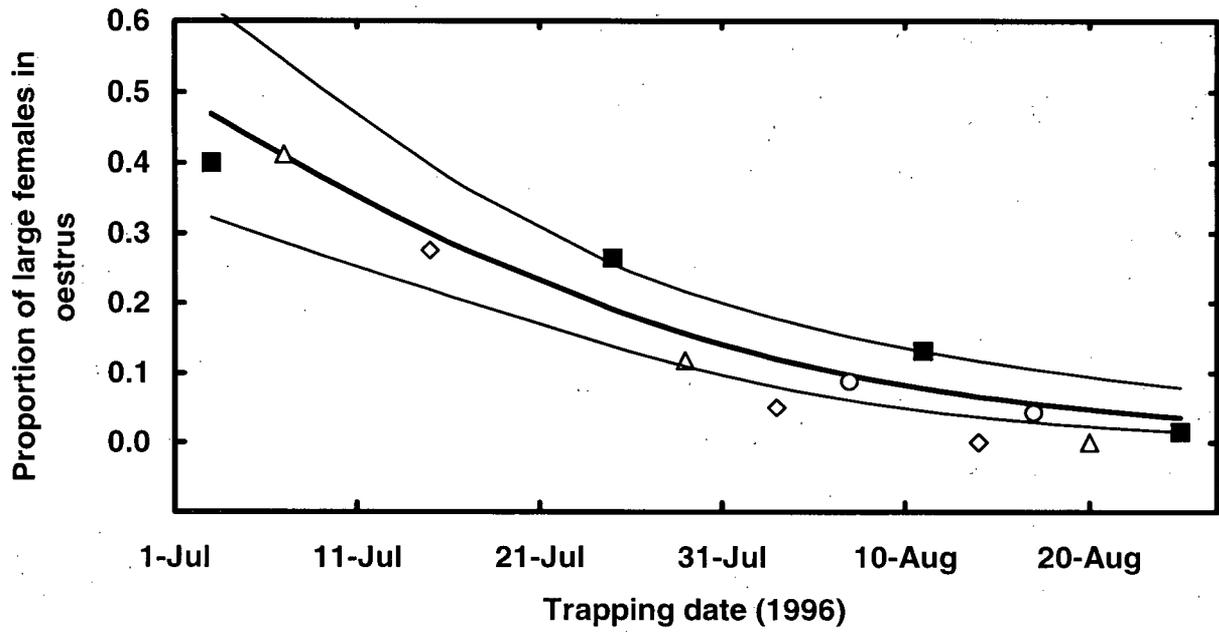
within each summer. In 1996 the proportion of large females recorded as in oestrus declined linearly (on a logit scale) throughout the summer ($t_{365} = 6.4$, $p < 0.0001$, Fig. 3-8a), from about 40% in late June to close to 0% in late August. In 1997 I used date as a categorical rather than a continuous variable because the proportion of females in oestrus did not change linearly throughout the summer (Fig. 3-8b). The proportion of large females recorded as in oestrus on all grids combined rose from 10% in June to 55% in July and fell to 31% in August (Fig. 3-8b). The difference between the proportions in oestrus in August and mid-June approached statistical significance ($t_{88} = 1.7$, $p < 0.1$), but the difference between the proportions in oestrus in August and July was not significant ($t_{88} = 1.3$, $p > 0.15$).

In snap-trapping surveys in June 1996 and 1997 the crude (observed) pregnancy rates of females were 82% ($n = 17$) and 70% ($n = 10$) respectively (Table 3-14). An observed pregnancy rate of 75% in *Dicrostonyx* equates to a true rate of 100%, because early stages of pregnancy cannot be detected macroscopically (Krebs 1964a). It is therefore probable that in June of both the peak and decline all mature females were pregnant. Only one female was trapped in each of July 1995 and July 1997; both were pregnant. In July 1996, however, only 27% of the 15 females trapped were apparently pregnant, even though 7 weighed ≥ 50 g; all the pregnant females were in this weight class. In addition, none of 7 telemetered females killed by predators between 12 July and 22 August 1996 were pregnant, though they weighed 53 – 112 g. In contrast, a female (55 g) killed on 12 August 1995 was pregnant, as were two (69 and 81 g) killed 29 and 30 July 1997. I found placental scars, indicating previous pregnancy, in both telemetered females in 1997 and in all but the smallest one (53 g) of the telemetered females in 1996.

None of the females trapped in June 1997 had placental scars from previous pregnancies. I did not assess placental scars in June 1996. However, 17 of 30 females trapped from 17 – 26

Fig. 3-8. a) The proportions of large (≥ 50 g) female *Dicrostonyx*, caught in live-traps, recorded as in oestrus in 1996. Lines show the proportions (and 95% confidence intervals) of females in oestrus on all grids, estimated by a logistic regression model with trapping date as a continuous variable. Diamonds, circles, triangles (Control grids) and filled squares (Exclosure) show the actual proportions of large females that were in oestrus on each trapping grid. b) The proportions of large female *Dicrostonyx* that were recorded as in oestrus in 1997. Crosses (×) show the proportions of females in oestrus on all grids, estimated by a logistic regression model with trapping period as a discrete variable. Error bars indicate 95% confidence intervals. Diamonds, circles, triangles (Control grids) and filled squares (Exclosure) show the actual proportions of large females that were in oestrus on each trapping grid. Points for Control 2 grid (circles) in late June and in August, and for Control 3 grid (triangles) in early July, represent single individuals.

a)



b)

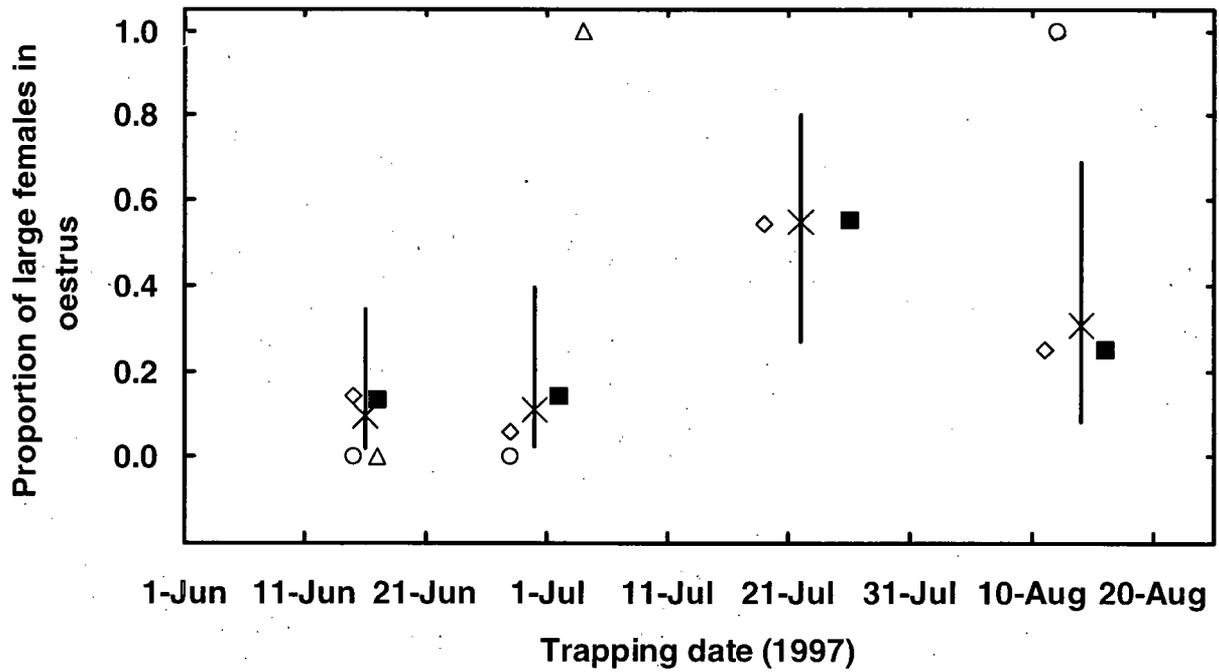


Table 3-14. Mass and reproductive condition (percentages pregnant and with placental scars), and mean litter sizes and mean number of resorbed embryos) of female *Dicrostonyx* caught in snap-traps at Walker Bay in June 1996 – 1997 and July 1995 - 1997. Placental scars were not assessed in June 1996. However, 17 of 30 females trapped on 17 – 26 June 1996 at other sites near Walker Bay had scars; scars occurred in 2 of 5 females weighing between 30 and 50 g and in 15 of 23 weighing ≥ 50 g (C.J. Krebs and A.J. Kenney, unpubl.).

Female <i>Dicrostonyx</i>		%			%		with scars		pregnant		litter size		embryos		
Year	Trapping dates	N	<25 g	25 - 50 g	>=50g	not assessed	with scars	not assessed	82	70	N	mean	se	N	% resorbed
1996	12 - 17 June	17	0	29	71	0	0	0	82	70	14	5.9	0.6	86	3.5
1997	17 - 23 June	10	0	40	60	0	0	0	70	70	7	6.1	0.7	43	0.0
1995	10 - 16 July	1	0	0	100	0	0	0	100	100	1	9.0	--	9	0.0
1996	11 - 16 July	15	20	33	47	40	40	40	27	27	4	4.3	0.5	18	5.6
1997	15 - 16 July	1	0	0	100	100	100	100	100	100	1	5.0	--	5	0.0

June 1996 at other study sites near Walker Bay had scars; scars occurred in 2 of 5 females weighing 30 – 50 g and in 15 of 23 weighing ≥ 50 g (C.J. Krebs and A.J. Kenney unpublished).

Mean June litter sizes were similar in 1996 and 1997 (mean \pm SE: 5.9 ± 0.6 and 6.1 ± 0.7 respectively, Table 3-14). In July 1996 the mean litter size (4.3 ± 0.5) was slightly but not significantly lower than in June. Sample sizes in July 1995 and 1997 were too small for me to compare litter sizes among years or trapping periods. I observed resorbed embryos in 1996 only; 3.5% were resorbed in June, and 5.6% in July (Table 3-14).

Sex ratio

The proportion of males trapped was higher in 1997 than on average in 1995 and 1996 (unplanned Helmert contrast, $t_{1073} = 2.18$, $p < 0.03$). This effect results from a difference in sex ratio of large animals only (Fig. 3-9), evident from the actual proportions of males captured). The percentages of large animals caught that were male were 25% in 1995, 34% in 1996 and 45% in 1997. More small and medium-sized lemmings than large ones were classified as males ($t_{1073} > 2.5$, $p < 0.01$) but this may have been a result of errors in determining the sex of immature animals. Neither grid nor period, nor any interaction terms remained in the model.

In snap-trapping surveys, a smaller proportion of males was caught in June 1997 (17%, $n = 12$, Table 3-15) than in June 1996 (32%, $n = 25$), but the difference was not significant (Fisher's exact test, $p > 0.4$).

Age structure

The proportion of adults caught in 1996 was lower than the mean of 1995 and 1997 (unplanned Helmert contrast, $t_{1071} = 2.8$, $p < 0.01$). The proportion of adults was higher in the periods June and June-July than in August, over all years ($t_{1071} > 3.7$, $p < 0.0005$). The proportion of adults in the Exclosure exceeded the mean proportion on the two Control grids

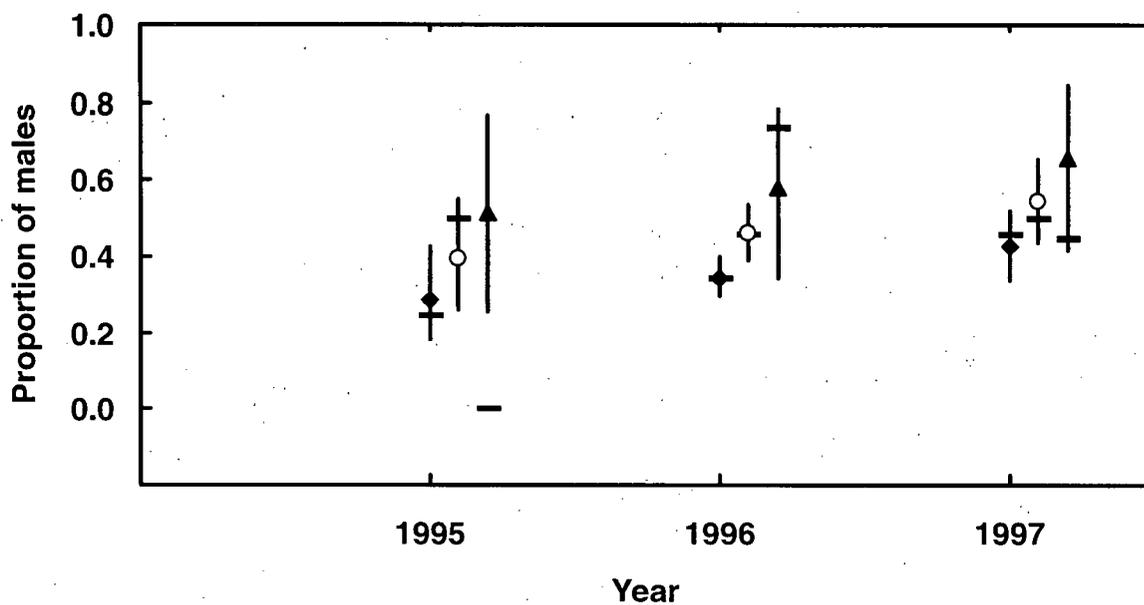


Fig. 3-9. The proportions of large (diamonds), medium-sized (open circles), and small (triangles) *Dicrostonyx* that were male, captured in live-traps in 1995, 1996, and 1997. Points show the proportions of male animals estimated by a logistic regression model. Error bars represent 95% confidence intervals. Horizontal lines show the actual proportions of animals of each size class that were male during each year.

Table 3-15. Sex ratio and size distributions of *Dicrostonyx* caught in snap-trap surveys at Walker Bay in June 1996 – 1997 and July 1995 – 1997. One carcass in each of June and July 1996 had been scavenged and was not weighed; in July the sex of the remains could not be determined.

Dicrostonyx caught in snap-traps

Year	Trapping dates	N	% Sex			% Size			
			male	female	not sexed	<25 g	25 - 50 g	>=50g	not weighed
1996	12 - 17 June	25	32	68		0	32	64	4
1997	17 - 23 June	12	17	83		0	42	58	
1995	10 - 16 July	4	75	25		0	25	75	
1996	11 - 16 July	30	47	50	3	33	30	33	3
1997	15 - 16 July	2	50	50		0	50	50	

($t_{1071} = 5.2$, $p < 0.0001$), but there was a significant interaction between year and grid. Grid (Exclosure) effects are discussed fully in Chapter 2.

In a model comparing the proportions of adult animals from Control grids 1 and 2 among years and sampling periods, the proportion of adults caught in 1996 was lower than in either 1995 or 1997 (treatment contrasts, $t_{578} = 2.2$, $p < 0.03$ and $t_{578} = 2.9$, $p < 0.005$). Across all years, a smaller proportion of adults was caught in June and in June-July than in August ($t_{578} = 2.8$, $p < 0.01$ and $t_{578} = 3.0$, $p < 0.005$). The interaction between year and sampling period was not retained in the model. The model fitted the data well (Fig. 3-10) except in June, when the actual proportions of adults were similar in 1996 (71%) and 1997 (68%), but only adults were caught in June 1995.

The proportions of snap-trapped *Dicrostonyx* weighing ≥ 50 g were similar in June 1996 and June 1997: 64% in 1996 and 58% in 1997 (Table 3-15). No lemmings weighing < 25 g were caught in June of either year. In July 1996 animals were distributed fairly evenly among the three size classes (< 25 g, $25 - 50$ g, and ≥ 50 g); one additional partially scavenged animal was not weighed but appeared to be > 25 g. In July 1995 and July 1997 no small animals were trapped and the proportions of large animals (≥ 50 g) were greater than in July 1996 (75%, $n = 4$ in 1995 and 50%, $n = 2$ in 1997), but sample sizes were small so the difference may not be important.

Mass of adult *Dicrostonyx*

Because of an interaction between year and period in the model of mass of adult *Dicrostonyx*, I modelled each period separately. Adults (> 40 g when first caught) weighed significantly less in June 1997 than in June 1996 ($t_{151} = 6.0$, $p < 0.0001$) (Chapter 2, Figs. 2-8b,c, 2-9). In June 1995 the mean mass of adults was also lower than in June 1996 but the difference was not statistically significant ($t_{151} = 1.5$, $p > 0.1$) (Chapter 2, Fig. 2-8a, b). The factor "sex"

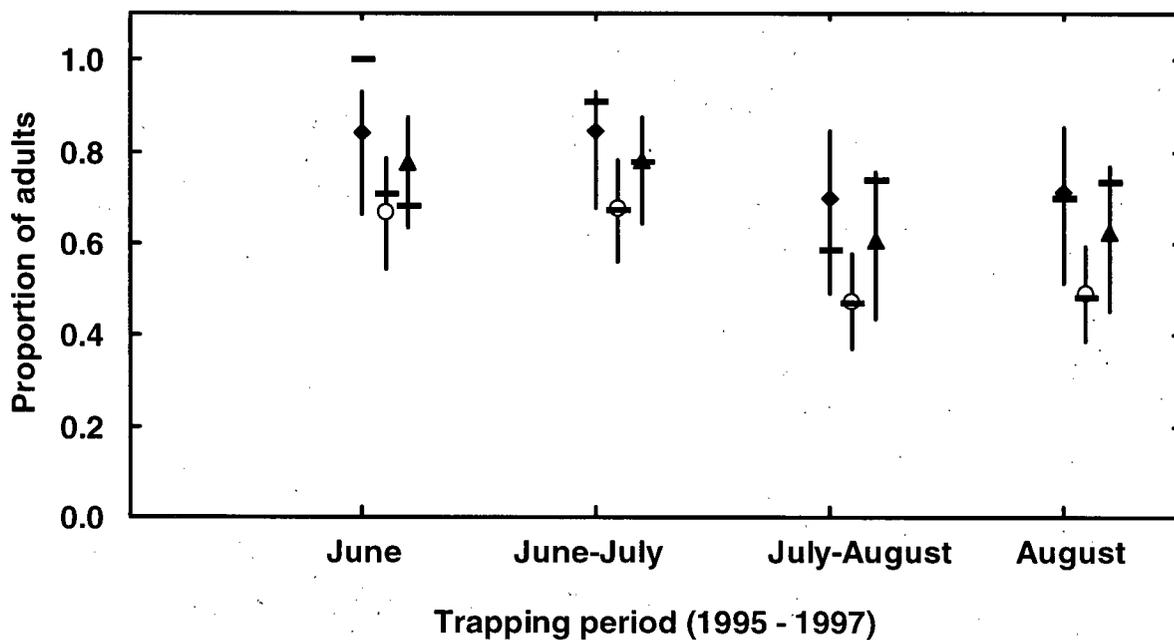


Fig. 3-10. The proportions of *Dicrostonyx* on Control grids 1 and 2 that were classified as adults (> 40 g) when first caught in live-traps, in four sampling periods in 1995 (diamonds), 1996 (open circles), and 1997 (triangles). Points show the proportions of adults estimated by a logistic regression model. Error bars represent 95% confidence intervals. Horizontal lines show the actual proportions of adults captured during each sampling period.

was not retained in the June model ($\Delta\text{AIC}_c = -0.02$), showing that the differences among years occurred in both sexes. The mean mass of adult males on Control grids in June 1995, 1996, and 1997 respectively was 75.4 ($n = 1$), 65.5, and 61.3 g; the corresponding figures for adult females were 67.8 g, 70.1 g, and 61.1 g. Mean mass of adults was higher in the Exclosure throughout 1996, 1997, and the latter part of 1995 (Chapter 2). In none of the models was there an interaction between grid and year or grid and sampling period; hence my conclusions about differences in mass apply to both the Exclosure and Control grids. Because year was not retained in the models of mass of adults for the periods June-July, July-August, or August ($-0.02 < \Delta\text{AIC}_c < 0$), I conclude that the difference in mass among years was evident only in June.

Population decline models

When the survival rates observed in August 1996 and June 1997 (Table 3-2) were used in the model of winter population decline; the predicted rate of decline (r) was -0.017 week^{-1} (Fig. 3-11a), less than half that observed on Control grids (-0.036 week^{-1}). However, a 30-day adult fall and winter (mid-August – mid-March) survival rate of 0.775, which was within the 95% confidence interval for July and August survival on Control grids, predicted a decline similar to that observed on Control grids (16 June density 3.4, $r = -0.037 \text{ week}^{-1}$; Fig. 3-11b). A 30-day fall (mid-August – mid-November) survival rate of 0.66, and winter survival of 0.876 as observed in August, predicted a similar result (16 June density 3.4, $r = -0.036 \text{ week}^{-1}$; Fig. 3-11c). This latter survival rate is within the rather large 95% confidence interval for survival of Control animals in August 1996, but is slightly below that for July 1996 (Table 3-2).

In contrast to the results of the model of the decline on Control grids, when the observed Exclosure survival rates (Table 3-2) were used in the model of winter population decline in the Exclosure, the modelled rate of decline (r) was -0.068 week^{-1} (Fig. 3-12a), almost double that observed in the Exclosure (-0.036 week^{-1}). Survival estimates in the Exclosure were very low in

Fig. 3-11. Modelled population declines (solid lines and crosses, ×) of untreated (Control) *Dicrostonyx* populations from August 1996 to June 1997. Dotted lines and filled diamonds, circles, and triangles show observed declines on Control grids. Open squares show mean Control densities. (a) Autumn and winter survival parameters set to Control grid estimates from August 1996, and spring survival set to Control grid estimate from June 1997 (Table 3-2). (b) Fall and winter survival (mid-August – mid-March) set to 0.775 per 30 days. (c) Fall survival (mid-August – mid-November) set to 0.66 per 30 days.

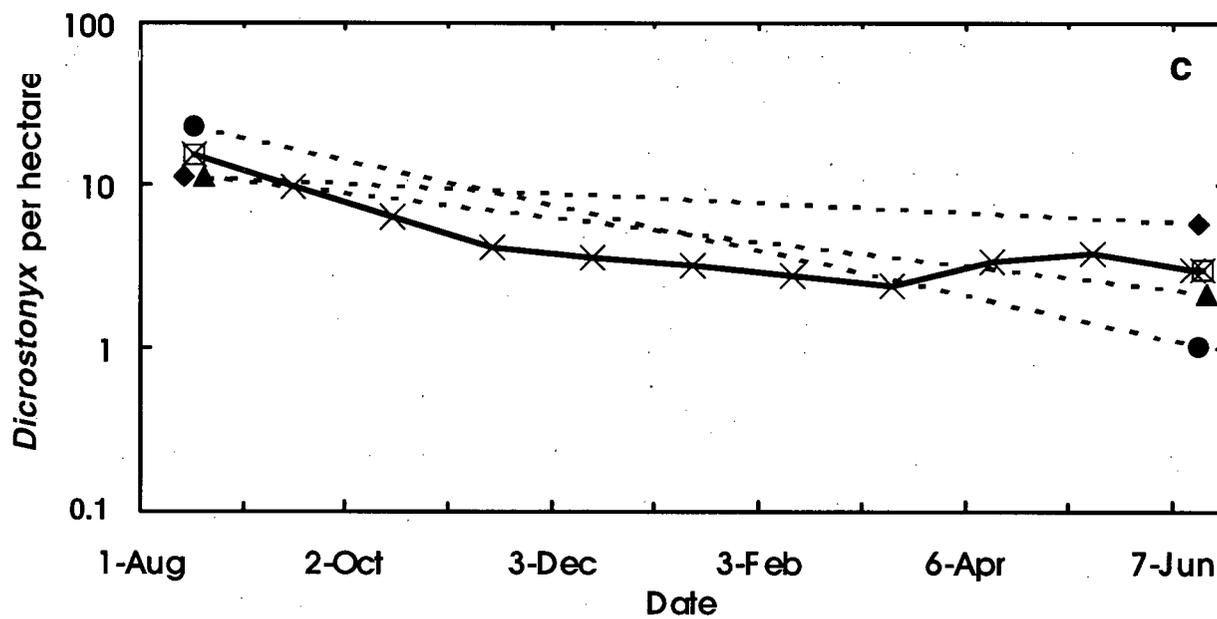
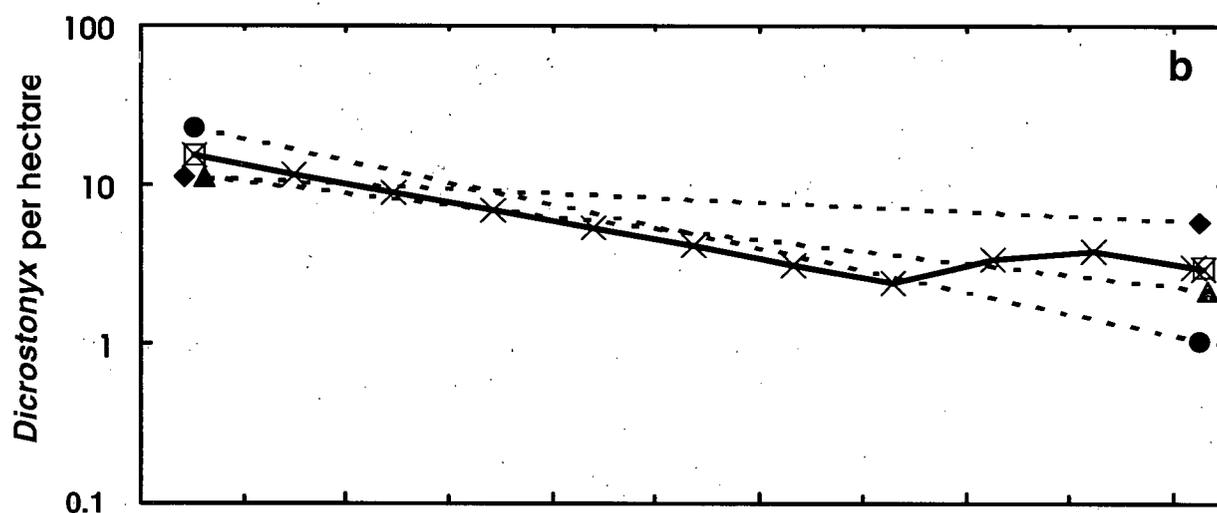
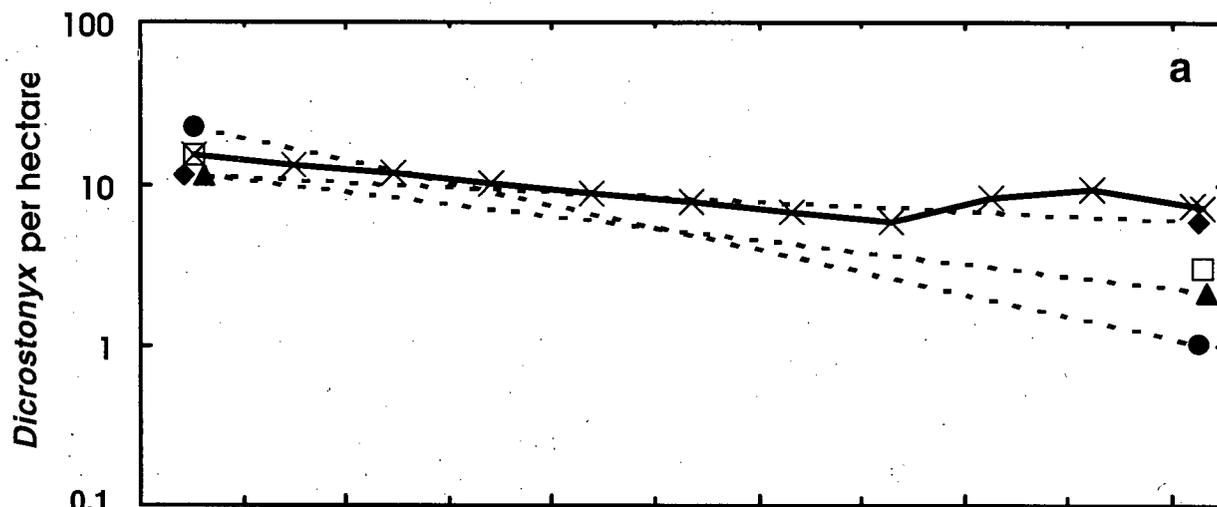
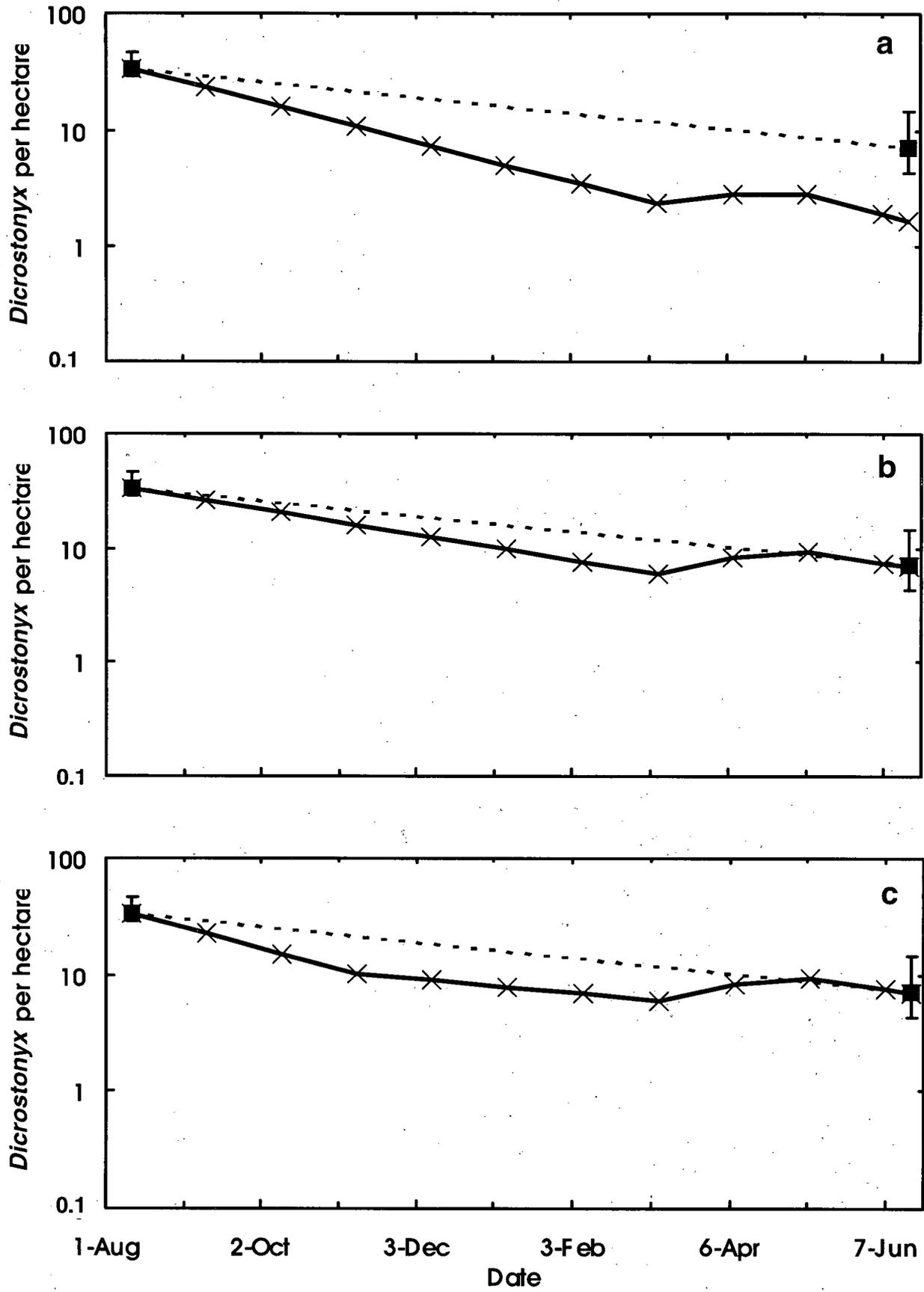


Fig. 3-12. Modelled population declines (solid lines and crosses, ×) of the protected (Exclosure) *Dicrostonyx* population from August 1996 to June 1997. Filled squares show observed Exclosure densities and 95% confidence intervals. (a) Survival parameters set to Exclosure estimates from August 1996 and June 1997 (Table 3-2). (b) Fall and winter survival (mid-August – mid-March) set to 0.78 per 30 days, spring survival set to June 1997 value estimated for Control animals (Table 3-2). (c) Fall survival (mid-August – mid-November) set to 0.67 per 30 days, winter and spring survival set respectively to August and June estimates for Control animals (Table 3-2).



August 1996 and June 1997 because of foxes entering the protected area (Chapter 2). Because the observed rate of decline was similar in the Exclosure to that elsewhere, it could be simulated with similar survival parameters to those described above for Control grids. A spring survival rate equal to that observed on Control grids and a fall and winter survival rate of 0.78, marginally higher than that used in the model for Control grids, predicted a decline similar to that observed in the Exclosure (17 June density 7.0, $r = -0.036 \text{ week}^{-1}$; Fig. 3-12b). A 30-day fall (mid-August – mid-November) survival rate of 0.67, slightly above that used in the model for Control grids, and winter and spring survival modelled as on Control grids, yielded a similar result (17 June density 7.1, $r = -0.036 \text{ week}^{-1}$; Fig. 3-12c). The modelled survival rates of 0.78 and 0.67 were within the large 95% confidence intervals for August survival in the Exclosure and on Control grids (Table 3-2, and see preceding paragraph).

The reproductive and juvenile survival parameters in all these models led to a predicted age structure in June 1997 of 54% over-wintered animals, 23% animals from spring litter 1, and 23% from spring litter 2. This distribution is acceptably close to the age structure indicated by the distribution of mass of lemmings trapped in June 1997 on Control grids. Forty-seven percent of the lemmings trapped weighed $> 50 \text{ g}$, 33% weighed $31 - 50 \text{ g}$, and 20% weighed $\leq 30 \text{ g}$. *Dicrostonyx* weighing 30 g are about 1 month old, and those $30 - 50 \text{ g}$ are between 1 and 3 months old (Chernyavski and Kiriushchenko 1979). This correspondence between the actual and predicted age structures provides assurance that the reproductive and juvenile survival parameters used were realistic.

The results of 1,000 Monte Carlo simulations of the full stochastic Crystal Ball decline model are shown in Fig. 3-13a and Table 3-16. The mean predicted density of *Dicrostonyx* in mid-June 1997 was 3.5 ha^{-1} (compared with the observed mean density of 3.4) with a standard deviation of 3.6 . The model predicted results within the range of those observed on Control grids ($1.1 - 6.7 \text{ ha}^{-1}$) in 54% of simulations (Fig. 3-13a). Hence, when uncertainty in the

Fig. 3-13. Results of 1,000 Monte-Carlo simulations, with Crystal Ball software, of the winter 1996 – 1997 decline in *Dicrostonyx* density. Graphs show the distribution of forecasted densities of *Dicrostonyx* (individuals ha⁻¹) on Control grids on June 16, 1997. Outliers refer to predicted densities above the maximum value on the X-axis. (a) Full model with all parameters allowed to vary as shown in Tables 3-1 to 3-3. Darker bars show the 54 percent of simulations that yielded results within the observed range of Control densities (1.1 – 6.7 ha⁻¹). (b) Reduced model with only adult survival parameters allowed to vary. Darker bars show the 66 percent of simulations that yielded results within the observed range of Control densities (1.1 – 6.7 ha⁻¹).

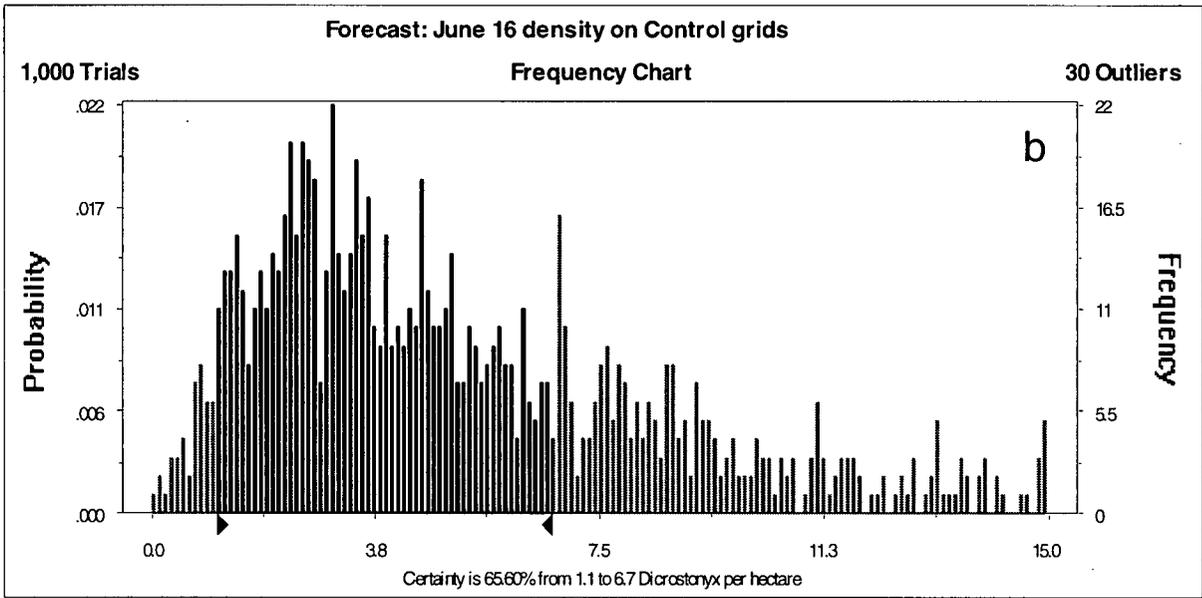
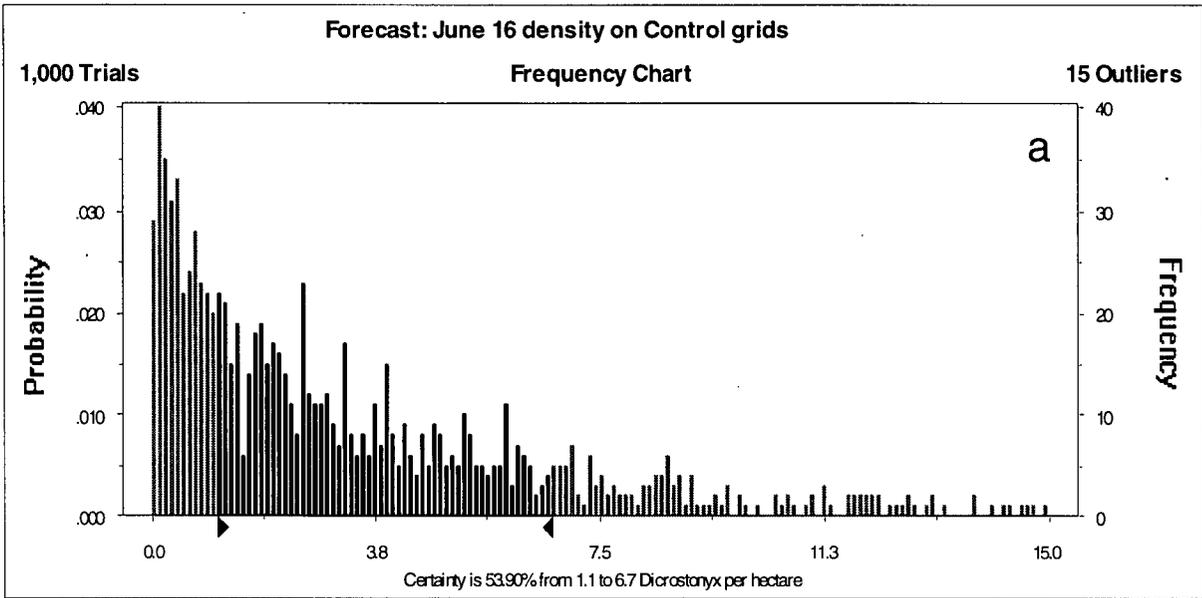


Table 3-16. Results of 1,000 Monte-Carlo simulations, using Crystal Ball software, of the winter 1996 – 1997 decline in *Dicrostonyx* density. Results are given for the full and reduced stochastic models (described in Methods). Statistics refer to the distributions of the forecasted density of *Dicrostonyx* (individuals ha⁻¹) on Control grids on June 16, 1997.

	<u>Full model</u>	<u>Reduced model</u>
Mean density	3.5	5.5
Median density	2.2	4.5
Standard deviation	3.6	4.1
Variance	13.2	16.5
Standard error of the mean	0.12	0.13
Skewness	2.0	1.8
Kurtosis	8.8	8.6
Coefficient of variation	1.1	0.7
Minimum density	0.0	0.1
Maximum density	30.3	36.6
Range width	30.3	36.5

parameter estimates was taken into account, the observed survival parameters combined with estimates of winter and spring reproduction from the literature predicted the observed decline well. However, because of the large uncertainty in most of the parameter estimates, this model often predicted extinction or severe declines (Fig. 3-13a).

The results of 1,000 Monte Carlo simulations of the reduced model, with only adult survival parameters allowed to vary, are shown in Fig. 3-13b and Table 3-16. The mean predicted density of *Dicrostonyx* in mid-June 1997 was higher than in the full model: 5.5 ha^{-1} (compared with the observed mean density of 3.4) with a standard deviation of 4.1. However, the model predicted results within the range of those observed on Control grids ($1.1 - 6.7 \text{ ha}^{-1}$) in 66% of simulations (Fig. 3-13b), and never predicted extinction (Table 3-16). In summary, with no variation in initial density or in reproduction parameters, and restricted variation in adult survival parameters (means equal to estimated values and variation less than the estimated 95% confidence intervals), this reduced model predicted June densities similar to those observed 66% of the time. These results provide further support for my above conclusion that the measured survival rates, even taking into account only part of the uncertainty in the estimates, can account for the observed decline.

Sensitivity analysis of the full stochastic model showed that the June density predicted by the simulation was most sensitive to variation in the following parameters: adult autumn survival, adult winter survival, initial density, and adult spring survival (Fig. 3-14). Adult autumn and winter survival together accounted for approximately 74% of the variation in the results of the model. The model was insensitive to variation in parameters of reproduction and juvenile survival. The survival of juveniles in the first month after leaving the nest accounted for 1.8% of the total variation. Other parameters related to reproduction and survival of neonates were jointly responsible for only 1.4% of variation in the predicted June density of *Dicrostonyx*. However, it is important to recognise that a key assumption of the model was that no

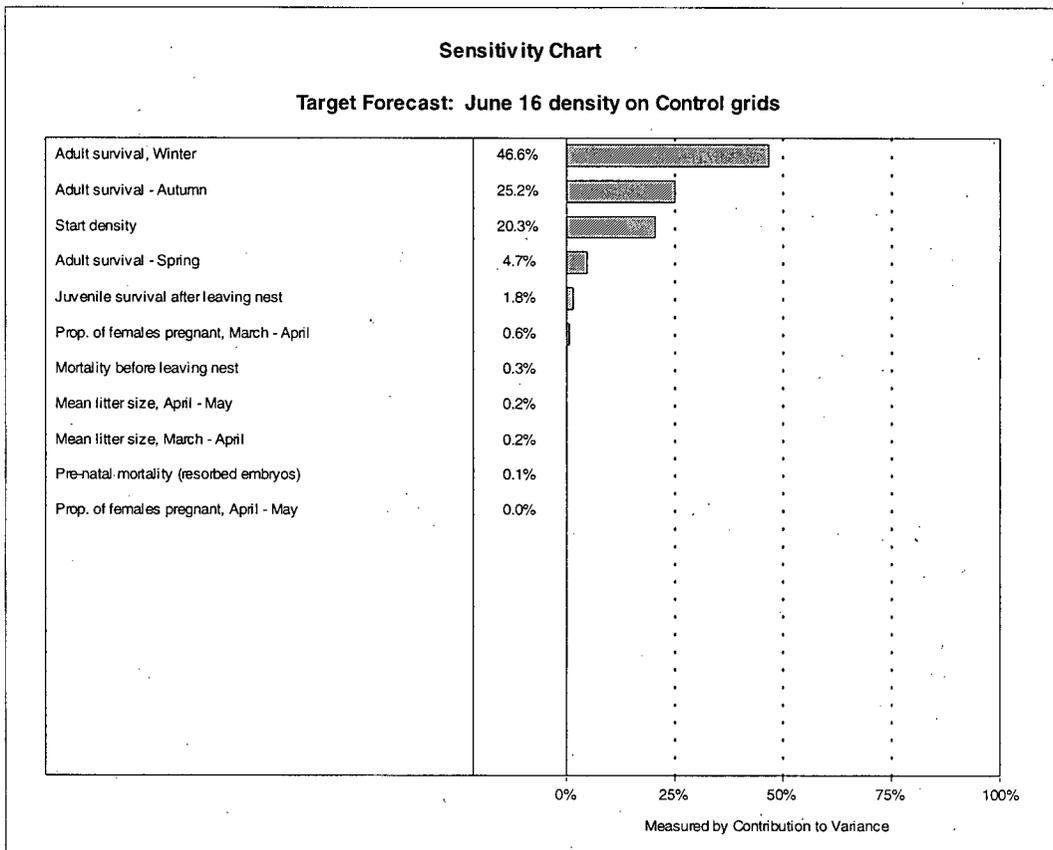


Fig. 3-14. Sensitivity analysis of the full Monte Carlo simulation model. Bars show the approximate percentage of total variation in the results of the model accounted for by each parameter.

reproduction occurred in winter, and because this parameter did not vary, its effect is not reflected in the sensitivity analysis.

DISCUSSION

The rate of population decline in the predator enclosure (-0.036 per week, Table 3-3b) was the same as that on Control grids in winter 1996 – 1997. In contrast, in the following summer, density began to increase within the Enclosure (+0.002 per week) while it declined on Control grids at an accelerated rate of -0.19 per week (Table 3-3b and Chapter 2). Hence my first prediction, that if predation is necessary to cause the population decline then the decline will not occur within the protected area, was not supported in the winter of the decline but was supported in the following summer. However, the conclusion for winter is weakened because the protective structure was less effective in deep snow and ineffective against ermine (Chapter 2). Further, arctic foxes and ermine entered the Enclosure in August 1996 (Chapter 2) and predation may have intensified in autumn as these predators responded to the enhanced density of lemmings within.

My second prediction, of a delayed density-dependent predation rate, was supported, since survival of *Dicrostonyx* was significantly lower in summer 1997 than in summer 1996, most deaths were due to predation, and predation rates were particularly high late in summer 1997 (Chapter 2; this chapter, Table 3-2). However, although the population declined substantially over winter, estimated survival in June 1997 equalled that in August 1996 (Table 3-2), suggesting that the predation rate did not rise until after the decline began. Did the predation rate increase in the winter following the peak summer? This question must be answered to test my third prediction, that the decline should be associated with a rise in predation rate. In the

following sections I estimate a winter predation rate based on the abundance of predators and their winter diets.

Numerical responses of lemming predators

Arctic foxes, ermine, rough-legged hawks, snowy owls, pomarine jaegers, and, to a small degree, short-eared owls all responded numerically to lemming abundance (Results and Tables 3-4, 3-5). However, snowy owls and rough-legged hawks did not seem to be important predators on the trapping grids in summer, perhaps owing to the low numbers of hawks and the distance of the nests of both species from the grids. Snowy owls, which were seen more often in late summer and fall, may have had a greater impact in autumn. Foxes were important predators in all three summers of the study, ermine in the peak and decline summers, pomarine jaegers in the peak only, and short-eared owls in the increase phase only. Only arctic foxes, ermine, and snowy owls would have been present in the winter of the decline, 1996 – 1997. Short-eared owls, pomarine jaegers, rough-legged hawks, and other birds of prey stopping on their southward migration, may all have been abundant until late in the autumn of 1996.

Functional responses of lemming predators

Foxes, snowy owls, rough-legged hawks, and probably glaucous gulls and peregrine falcons responded functionally to lemming density (Figs. 3-3, 3-4, 3-5). The apparent Type II response (Holling 1959a) of arctic foxes (Fig. 3-3) contrasts with the Type III response of red foxes observed by Reid *et al.* (1997). This pattern, and their inability to breed at low lemming densities (Table 3-4), suggest that arctic foxes in this region may be more specialised lemming predators than were the red foxes at Pearce Point (western N.W.T.). Reliance on lemmings was particularly evident in juvenile arctic foxes, as in 1996 their scats contained remains of no other prey types. In some regions, however, arctic foxes live primarily on carrion and avian or marine

prey (Hersteinsson and Macdonald 1982, 1996; Frafjord and Prestrud 1992, Prestrud 1992, Anthony 1997). Their apparent specialisation on lemmings on the Kent Peninsula may therefore be related to a shortage of other prey.

Predation in winter by arctic foxes

The estimated mean biomass of *Dicrostonyx* ingested per adult fox scat remained high in winter 1996-7 (41.1 g compared with 47.8 g in August 1996). However, assuming low winter reproduction of lemmings (100:1 ratio of adults to juveniles), the estimated average number of *Dicrostonyx* consumed per day per fox in winter (2.6) was much lower than in summer 1996 (up to 6.9, Table 3-10). My estimate of the total consumption of lemmings by foxes in winter 1996-7 (Table 3-10) is rough because it depends on an arbitrary assumption of linear dispersal throughout winter of juvenile foxes (i.e. over a 10-month period about one fox dies or emigrates monthly). This assumption leads to an estimate of average consumption by all foxes of 18.4 lemmings day⁻¹ throughout winter, or 0.19 lemmings ha⁻¹ 14 days⁻¹.

Predation in winter by ermine

The number of lemming nests occupied by ermine in winter 1996-7 (4%, Table 3-6) was low compared with observations in Greenland of 9% and 14% in two declining years (Sittler 1995). At Barrow, Alaska least weasels (*Mustela nivalis*) occupied 35% of lemming nests in a decline year (MacLean *et al.* 1974). Since I knew of several ermine near the trapping grids in August 1996, and one marked female and one unmarked male in June 1997, at least two ermine probably lived in the area throughout winter. Estimates of the home range size of North American ermine, which have smaller bodies and ranges than do European ermine, vary considerably depending on habitat, food availability, and the abundance of conspecifics (Fagerstone 1987). Ranges of males and females overlap (Fagerstone 1987). Average home

range sizes in Ontario in the non-breeding season were 10.5 ha for females and 23 ha for one male (home ranges of breeding males averaged 20.7 ha; Simms 1979). Home ranges in California were smaller (Fitzgerald 1977), but in central Alberta home ranges were much bigger: 79.9 ha for females outside the breeding season and 141.6 ha for males, combining both breeding and non-breeding periods (K. Lisgo, unpublished). To recognise both the high density of prey at Walker Bay in 1996 – 1997, and the large size of northern ermine, I averaged these estimates to obtain 45.2 ha for females and 82.3 ha for males. I assumed that the trapping grids lay within non-overlapping ranges of one male and one female.

Gessaman (1972) estimated that one 60-g lemming is equivalent to 77 kcal of energy (322 kJ). I estimated the daily food requirements of ermine by extrapolating from Brown and Lasiewski's (1972) predictions of the energy requirements of long-tailed weasels (*Mustela frenata*) as a function of mass and ambient temperature. The mass of ermine varies considerably and increases at high latitudes, so I used the mean mass of 7 females (mean \pm SE: 113 ± 6.7 g) and 3 males (154.5 ± 17.3 g) weighed at Walker Bay in 1996 and 1997. These means are probably underestimates since many of the weighed animals were subadults. The results of these calculations were that at -10°C , a female ermine would need 1.3 60-g lemmings daily, and a male would need 1.4. The winter air temperature at Walker Bay is much lower than -10°C , but by using lemming winter nests ermine may attain a higher ambient temperature (MacLean *et al.* 1974). These calculations lead to an estimated consumption by ermine of 0.34 lemmings ha^{-1} 14 days⁻¹. Because ermine cache prey for future use (Oksanen *et al.* 1985), they may take more prey in some periods but less when hoarded food is retrieved.

Predation in winter by snowy owls

I do not know how many snowy owls foraged in the area in winter. Many of the large number present in August – September likely emigrated or died during winter, and others

immigrated in spring. One owl remaining in the 25-km² home range assumed for foxes (1,365 ha of *Dicrostonyx* habitat) in mid-winter, eating 3.3 *Dicrostonyx* day⁻¹ as I calculated from winter owl pellets (Fig. 3-5), would eat 0.034 *Dicrostonyx* ha⁻¹ 14 days⁻¹.

Total winter predation rate

The above estimates of *Dicrostonyx* eaten by arctic foxes, ermine, and snowy owls sum to a total winter consumption of 0.6 *Dicrostonyx* ha⁻¹ 14 days⁻¹. Based on an average winter density of 9.6 lemmings ha⁻¹, this estimate equates to a predation rate of 0.06 14 days⁻¹ and 30-day survival rate of 0.88. This estimate is, of course, very rough, but is similar to my estimates of summer survival rates based on radio-telemetry (Table 3-2). Estimated winter predation based on the above calculations is shown in Fig. 3-15.

These estimates offer no evidence of an increased predation rate in the winter following the peak. Hence my third prediction, that the decline should be associated with an increased predation rate, is not supported. It is, however, possible that predation rates rose temporarily in autumn when foxes and owls were abundant and before the snow was deep and densely packed. Both foxes and snowy owls must find it difficult to hunt lemmings under hard snow. Ermine were probably also more abundant in autumn, before winter mortality occurred. As well, some migratory predators were present in autumn and those passing through from further north may have stopped for longer than in other years because of the abundance of prey.

A constant number of predators with Type II functional responses in the absence of prey reproduction would lead to an increasing rate of predation as lemming numbers declined (Holling 1959a), i.e. inversely density-dependent or depensatory predation. In this case the predation rate would have been higher in late winter than in fall. A moderate rate of decline in numbers of predators does not preclude depensatory predation, but if predator numbers drop rapidly or functional responses are Type III, the predation rate may decrease (Holling 1959a).

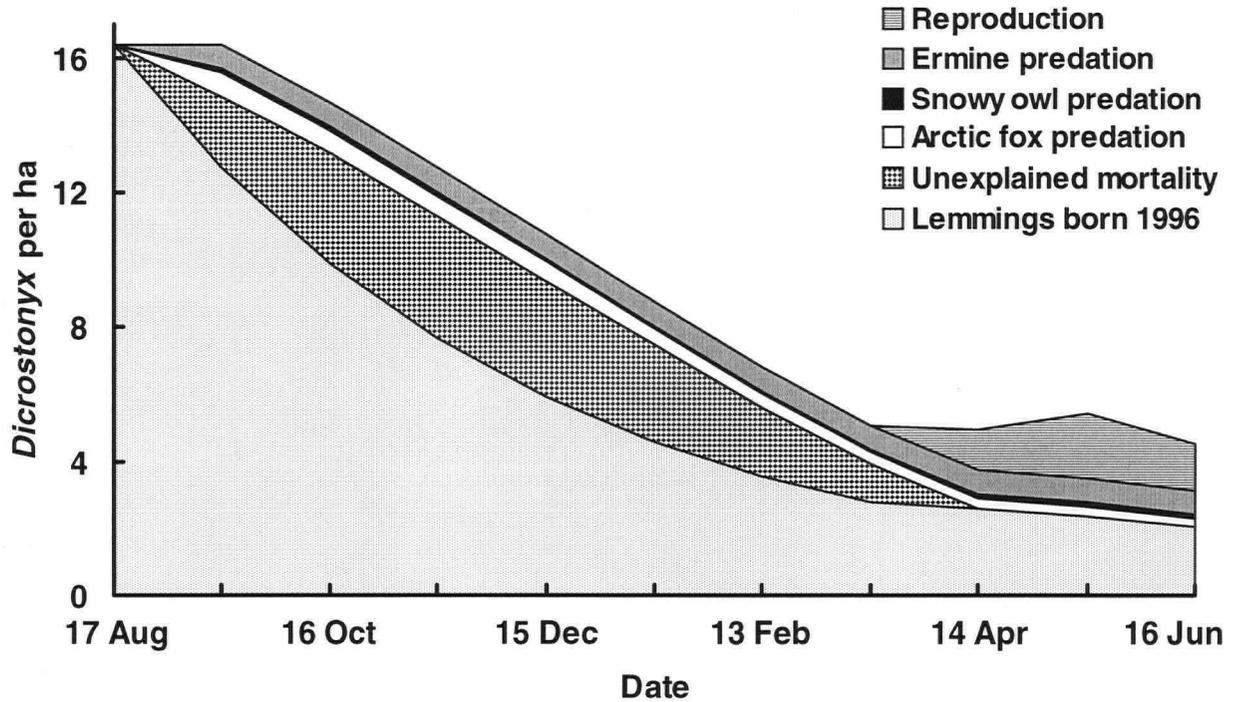


Fig. 3-15. Estimated 1996 – 1997 winter predation by arctic foxes, snowy owls, and ermine on *Dicrostonyx*, based on estimates from scats, pellets, and metabolic requirements (see Discussion), compared with modelled predictions of the population decline. I assumed linear dispersal of foxes as described in the text, 2 snowy owls per 25 km² from August – October and April – June and 1 at other times, and a constant number of ermine (2, see text). “Lemmings born 1996” shows the modelled population decline of adults as shown in Fig. 3-11b (fall and winter survival 0.775, spring survival 0.877). Reproduction shows spring-born individuals from the same model. Unexplained mortality illustrates the gap between estimated predation and the modelled mortality. The initial and final population densities equal the observed mean Control densities in mid-August 1996 and mid-June 1997 respectively.

Ermine are particularly likely to continue to exploit lemmings at low density before emigrating, because ermine are adapted to hunt under the snow (Fitzgerald 1977) and are more specialised than foxes and cannot emigrate as far as owls can. However, the predation rate on Control grids was not lower in June 1997 than in 1996 (Table 3-2), and without knowing rates of emigration or death of predators, I cannot estimate changes in predation rate during fall and winter.

With no evidence that an increased predation rate initiated the population decline, we must look for other causes. The decline could have been initiated either by an increase in sources of mortality other than predation, or by a decrease in reproduction. The mortality rate may have risen in autumn 1996 owing to deteriorating weather and competition for food as plant growth slowed. I observed but did not quantify damage from lemmings gnawing on willow bark (*Salix lanata* and *S. arctica*) and browsing on shoots of *Dryas integrifolia*. My survival estimates show no evidence of an increase in mortality before the end of August (Chapter 2 and Table 3-2).

Cessation of reproduction in the peak summer

Collared lemmings stopped reproducing by the end of July in the peak summer, but were still reproducing in late August of the increase (1995) and decline (1997) years. This difference was apparent from the proportions of males and females in reproductive condition (Figs. 3-6, 3-7), the lack of spermatogenesis and low rate of pregnancy in lemmings snap-trapped in July 1996 (Tables 3-13, 3-14), and the absence of pregnancies in telemetered females killed by predators in July and August 1996 (Results). As well, the proportion of large females that were in oestrus in 1996 decreased monotonically to almost zero by the end of summer, whereas no such decrease occurred in 1997 (Fig. 3-8).

The few studies of winter reproduction in *Dicrostonyx* report no winter breeding after peak summers, until spring (April – May) (Krebs 1964a, Chernyavski 1979, Chernyavski and

Kiriushchenko 1979). MacLean *et al.* (1974) deduced from the abundance of lemming winter nests (most of *Lemmus trimucronatus*, but a few of *Dicrostonyx*) that winter breeding was reduced after peak years, and attributed a population decline to reduced breeding combined with non-predation mortality. Sittler (1995) concluded from the paucity of small faecal droppings in winter nests that reproduction was low after a peak summer, but suggested that this effect could have resulted from disproportionate predation by ermine on oestrous females. Only spring breeding of *L. lemmus* after a peak has been reported [review of winter reproduction in Scandinavian microtines, Hansson (1984); the January – April breeding observed by Henttonen and Järvinen (1981) occurred before an early summer peak, not after as reported in the review].

Without reproduction, a decline must occur if there is mortality. The decrease in reproduction, but not in survival, in August of the peak implies that the lemming decline was initiated not by increased predation, but by cessation of reproduction. Krebs (1964) pointed out that in the absence of winter and spring breeding, even a low rate of mortality (e.g. 30-day survival of 0.75 – 0.90) would result in a substantial population decline during the 10-month arctic winter. My simple population decline models predicted the observed winter decline even assuming spring breeding, and with adult survival parameters within the range of values estimated from radio-telemetry in summer.

Predictions of the population decline models

The deterministic population decline model (Fig. 3-1) assumed no winter reproduction, spring reproduction from mid-March to mid-May (Table 3-1), and spring adult survival equal to the June 1997 value (0.877, Table 3-2). With fall and winter 30-day survival rates of 0.775, or lower rates of survival (0.66) in the first 3 months of autumn, the model predicted the observed decline. These survival rates are within the 95% confidence intervals for survival in July and August 1996 on Control grids (Table 3-2). The reduced stochastic model set mean adult autumn

and spring survival rates to the observed August 1996 and June 1997 values respectively, and allowed them to vary from the upper 95% confidence limits of those parameters, to values higher than the lower 95% confidence limits. This model predicted the observed decline 66% of the time (Figs. 3-1, 3-13b). None of the modelled survival rates were low compared with those estimated for other small mammals, even in phases other than the decline (Krebs and Myers 1974, Batzli *et al.* 1980).

Factors contributing to the winter decline

In summary, the beginning of the decline was associated with decreased reproduction but not decreased survival. My rough estimate of the winter predation rate based on fox scats, owl pellets, and the energy requirements of ermine approximated estimates of predation rates obtained in summer 1996 from radio-telemetry. Simple population decline models showed that with no reproduction until spring, low mortality rates could lead to the observed decline. The winter decline was not prevented within the predator enclosure. These results imply that predation was not a necessary cause of the population decline, but are not conclusive because the effectiveness of the predator enclosure was reduced in fall and winter. Whether the rate of decline would have been less in the complete absence of predation depends on the extent to which other sources of mortality compensated for the removal of predation. Some compensatory mortality of telemetered lemmings was observed in the Enclosure at high population density in 1996, although less occurred in 1997 (Chapter 2); compensation may occur to a greater extent at high density. I cannot draw a firm conclusion about whether predation was a necessary cause of the winter population decline, but I propose that a decreased reproductive rate may have been a necessary cause.

Factors contributing to the summer decline

The rate of decline was much higher in the summer of 1997 (-0.19 per week on Control grids) than in the previous winter (-0.036 per week, Table 3-3b). This pattern has been termed a Type L decline (Chitty 1996, p. 94). The faster decline in summer appeared to be due to a higher rate of predation, although I cannot pinpoint with precision when the more rapid decline began. Delayed density-dependent predation mortality was observed between the peak and decline summers: survival was significantly lower in summer 1997 than in summer 1996, and predation rates were particularly high in July and August 1997 (Chapter 2; this chapter, Table 3-2). The predator reduction experiment showed that predation, primarily by ermine, was necessary and possibly sufficient, to limit the lemming population in the summer of the decline (Chapter 2). While the population declined on Control grids, it began to increase within the Exclosure ($r = +0.002$ per week in summer, Table 3-3b). Ermine were not prevented from entering the Exclosure, but no known predation by ermine occurred in the treated area (Chapter 2), either because I had removed two ermine in 1996, or because of a naturally patchy distribution of these animals. Ermine were the only predators with a delayed numerical response to lemming density; they were abundant in both 1996 and 1997. In the peak year the lemming population may have been too dense to be regulated by ermine predation (Sinclair *et al.* 1992). My conclusion that predation by ermine was a necessary cause of the summer decline is supported by the fact that the lemming population did not decline in 1995 when ermine were rare, even though the June population density was similar to that in 1997 (Chapter 2, Fig. 2-2).

I showed in Chapter 2 that before the protective predator exclosure was built, demographic parameters did not differ between the Exclosure and Control grids, suggesting that the different population dynamics between the treatments should not be the result of differences in the habitats. Still, my comparison of population trajectories between the Exclosure and Control sites is weakened by the lack of replication of the experimental treatment. The results of

this study, together with the experimental results of Korpimäki and Norrdahl (1998), show the potential of predator-removal experiments to test hypotheses about the role of predation in the dynamics of cyclic microtines. Repeating my experiment on lemmings, with more replication and an improved protective structure, has a very good chance of yielding conclusive results.

Sources of error in estimating diets of lemming predators

My estimation of per hectare consumption of lemmings by arctic foxes relies on many untested assumptions. First, the area of the foxes' foraging range was based on the literature and a rough estimate of the proportion of *Dicrostonyx* habitat within that area. Second, conversions of biomass excreted to that ingested were based on red fox data (Appendix 1). Third, the defecation rate of arctic foxes was based on rates for red foxes, captive arctic foxes, and unquantified observations. Fourth, my conversion of unidentified prey biomass in scats (which occurred in the low and increase years only) to ingested biomass may have been inaccurate. Other possible sources of error discussed by Reid *et al.* (1997) were (1) an overestimate of consumption by juvenile foxes because they digest food less completely than do adults, and (2) an underestimate of consumption of juvenile lemmings because some small bones may be entirely digested (Lockie 1959). My highest estimated daily consumption of 7.4 lemmings (*Dicrostonyx* plus *Lemmus*, both adults and juveniles; Results and Table 3-10) by adult foxes in the peak summer may be an underestimate. Captive wild arctic foxes consumed on average 530 kcal day⁻¹ (2219 kJ day⁻¹; Frafjord 1993), equivalent to 6.9 60-g lemmings (Gessaman 1972), and Dorogoy (1983) estimated that adult arctic foxes ate 10 lemmings daily during a peak. In contrast, my estimate of 4.3 lemmings eaten day⁻¹ by juvenile foxes corresponds better with Dorogoy's (1983) estimates that juveniles needed up to 3 lemmings daily in the first month after weaning and 8 – 10 in the next month. Hence the conversion factor of 28 (Appendix 1) for arctic

fox digestion of lemming biomass might be too low for adult arctic foxes but appropriate for juveniles.

Although the estimated absolute daily consumption of lemmings per fox may not be accurate, comparing the relative numbers eaten among years of different lemming densities – the functional response; discussed below – is valid. The fit of a Type II function was robust to smaller differences among defecation rates in periods of high and low lemming abundance (Fig. 3-3). However, conclusions based on scats from the low year, 1994, may be misleading because of the chance of scats from previous years being included. As well, as mentioned above, in July 1996 the sample of adult fox scats may have included some juvenile scats.

These calculations probably underestimate the number of lemmings killed by foxes when lemmings were abundant, because foxes engage in surplus killing (Oksanen *et al.* 1985) by hoarding prey for later use (Seton 1929, Pedersen 1962, Garrott and Eberhardt 1987, Sklepkovych and Montevecchi 1996) and by killing apparently unwanted prey (pers. obs.). During 1996 I found four telemetered lemmings in the predator enclosure that had apparently been killed by foxes and left lying on the tundra. Conversely, consumption rates after periods of high abundance may be over-estimated, because of retrieval of cached prey.

In spite of these sources of error, my estimates of lemming mortality from fox predation corresponded very well with estimates based on radio-telemetry in the summer sampling periods from July 1996 to early July 1997 (Table 3-11). During these periods sample sizes were high, and I was able to identify all prey items in the scats (Table 3-7). The different biases may have cancelled each other during these periods. I conclude that interpolating these results to estimate fox predation in the 1996 – 1997 winter decline period was appropriate.

Sources of error in the estimation of the functional responses of rough-legged hawks and snowy owls were less grave. The most serious was my arbitrary choice of a casting rate by snowy owls of 1.55 pellets day⁻¹, based on the short-eared owl literature, and 1 pellet day⁻¹ for a

food-stressed owl in 1994. However, my estimated daily consumption by snowy owls of about 5 or 7 lemmings day⁻¹ (both species, see Results) corresponds well with published estimates. Gessaman (1972) concluded from bioenergetics that an adult snowy owl needed 6.6 60-g lemmings day⁻¹ in cold weather (-29°C) and 4 in autumn (-5 to +5°C). Pitelka *et al.* (1955) found that once growth of a captive young owl stabilised it ate the equivalent of 5.4 60-g lemmings day⁻¹, and Dorogoy (1983) concluded that an adult bird on Wrangel Island ate 5 lemmings day⁻¹.

Sex ratio

The higher proportion of males among large lemmings caught in 1997 could have been the result of a lower winter mortality rate of males than of females. MacLean *et al.* (1974) proposed that in winter ermine preyed more heavily on breeding females, identifiable by their larger winter nests, accounting for higher proportions of males after increase winters. Males were also less vulnerable than females to summer predation by red foxes (Reid *et al.* 1997), but male brown lemmings were more vulnerable than females to summer predation by snowy owls (Pitelka *et al.* 1955, Batzli *et al.* 1980).

Age structure

Since there was no evidence of larger litters in the peak than in other years (Table 3-14), the smaller proportion of adults than juveniles trapped in the peak could have resulted from better juvenile survival in the peak phase. The mortality rate of telemetered juveniles was very low in the peak (Blackburn *et al.* in press). However, the low proportion of juveniles in the increase phase (1995) is surprising, since in fluctuating populations juvenile mortality is generally highest in peak and decline phases (Krebs 1993). I have no data on juvenile survival in 1995. Possibly, by moving traps between secondary trapping sessions in 1996 and 1997, but not

in 1995 (Chapter 2, Methods), I increased the chance of catching juveniles that territorial adults might otherwise might have prevented from entering traps.

Mass of adult *Dicrostonyx*

My observation that adult collared lemmings were heavier, on average, in June of the peak than in June of the decline phase (Chapter 2, Figs. 2-8b,c, 2-9) is consistent with the "Chitty effect" (Chitty 1952), that over-wintered microtines in peak populations tend to be large. I also found that adults were larger in the Exclosure than on Control grids throughout the experiment (Chapter 2, Figs. 2-8, 2-9). Alternative hypotheses to account for these size differences are discussed in Chapter 2.

Summer and winter reproduction in lemmings

An abbreviated breeding season during the peak phase is typical of cyclic microtines (Krebs and Myers 1974), and was observed in *Dicrostonyx* by Krebs (1964) and Chernyavski (1979). Several studies of lemmings reported no early cessation of reproduction in the peak, but found lower rates of maturation of *Dicrostonyx* or *Lemmus trimucronatus* (Pitelka 1973, Fuller *et al.* 1975b, Batzli *et al.* 1980). It is not known why lemmings stop reproducing at high density. Alternative hypotheses include declines in food abundance or quality (Batzli 1985), physiological effects of aggression or crowding (Christian and Davis 1966), high risk of predation (Korpimäki *et al.* 1994, Ylönen 1994), and other cyclic genetic or phenotypic changes in the individuals (Chitty 1960). Two hypothetical ultimate causes leading to a reproductive response to the presence of nearby conspecifics are avoidance of breeding with relatives and risk of infanticide (Wolff 1997).

Whether lemmings never reproduce in the winter after a summer peak is not known. Like the early cessation of reproduction in the peak summer, the lack of winter reproduction

could result from intrinsic changes or to responses to environmental conditions. Agrell *et al.* (1995) showed that poor growth and reproduction of experimentally introduced voles (*Microtus agrestis*) was associated with previous high vole density, and suggested that the abundant voles in the previous year might have impacted food quality.

It has been hypothesised that winter reproduction occurs only during the increase phase in arctic and subarctic small mammals, and that therefore winter breeding is important in the generation of cycles (Kaikusalo and Tast 1984). However, it is not easy to procure animals for testing when densities are low. Lemmings may breed in all winters except when densities are high, and the cessation of breeding, combined with winter mortality, may lead to over-winter declines. Obviously, much more information is needed about winter reproduction in lemmings.

The importance of predation by mustelids

It has been proposed that predation by mustelids, which are specialist rodent predators, is a necessary cause of declines in cyclic small mammal populations in Fennoscandia (e.g. Henttonen *et al.* 1987, Hanski *et al.* 1993, Korpimäki 1993, Korpimäki and Norrdahl 1998). When Norrdahl and Korpimäki (1995b) removed avian predators or least weasels only the density of voles did not increase, but when they removed both avian predators and mustelids (least weasels and ermine), vole densities increased in summer within the removal areas when they were declining elsewhere (Korpimäki and Norrdahl 1998). Mustelids have also been implicated in declines of voles and lemmings in North America (Maher 1967, MacLean *et al.* 1974, Pitelka 1973, Fitzgerald 1977) and of lemmings in Greenland (Sittler 1995).

My results do not support the hypothesis that predation was a necessary cause of the population decline in winter. None of the three predictions of this hypothesis were met in winter. First, the decline occurred at the same pace within and outside a predator enclosure. Second, a delayed density-dependent rise in predation rate was not evident until the following summer.

Third, the beginning of the decline was not associated with an increase in predation rate. Instead, the decline seems to have been initiated by cessation of reproduction by the end of July in the peak summer, implying that predation was not a sufficient cause of the winter decline. But because the effectiveness of the predator exclosure was reduced in winter, I cannot with certainty refute the hypothesis that predation was a necessary cause of the winter decline. The contribution of predation to the decline depends on the extent to which sources of winter mortality were compensatory.

The results do support the hypothesis that predation was a necessary cause of the population decline in the following summer, when all three predictions of the hypothesis were met. First, the decline was reversed within the predator exclosure in summer 1997. Second, a delayed density-dependent increase in predation rate occurred in summer 1997 compared with the previous summer. Third, the steeper summer decline was associated with this increase in predation rate. I conclude that the decline was initiated late in the peak summer (1996) by cessation of reproduction, but that a high rate of predation, primarily by ermine, was necessary to accelerate and extend the decline in the following summer (1997). Predation was therefore regulatory in summer 1997, but may not have been regulatory in autumn or winter.

In lemming populations, the decline phase can occur in any season at a low or high rate (Krebs 1993). For example, brown lemmings at Barrow crashed in spring and summer, associated with heavy predation by avian predators and least weasels (Pitelka 1973, Batzli *et al.* 1980).

Therefore my conclusions might apply to only certain declines. Alternatively, all declines from high density may have in common reduced breeding and elevated rates of mortality due to various causes, such as shortage of food or space and the numerical and functional responses of predators. The extent to which changes in reproduction and the different causes of mortality contribute to declines may vary among species, locations, and years.

CHAPTER FOUR

FUNCTIONAL AND NUMERICAL RESPONSES OF PREDATORS TO CYCLIC LEMMING ABUNDANCE: EFFECTS ON LOSS OF GOOSE NESTS

INTRODUCTION

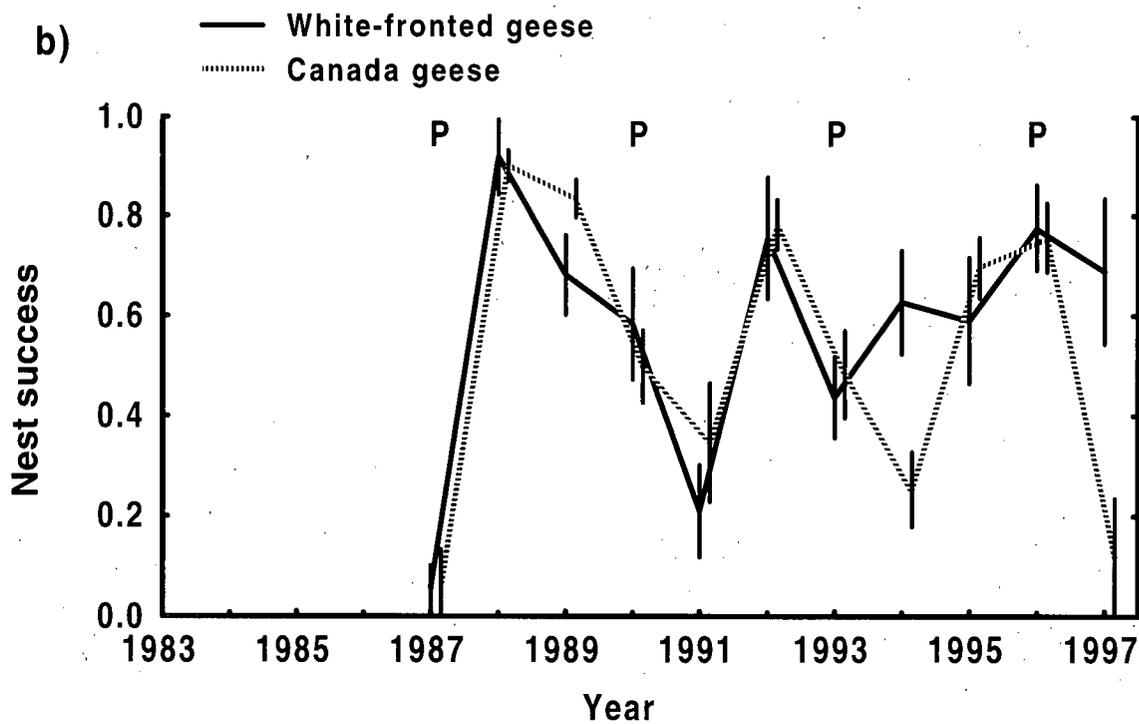
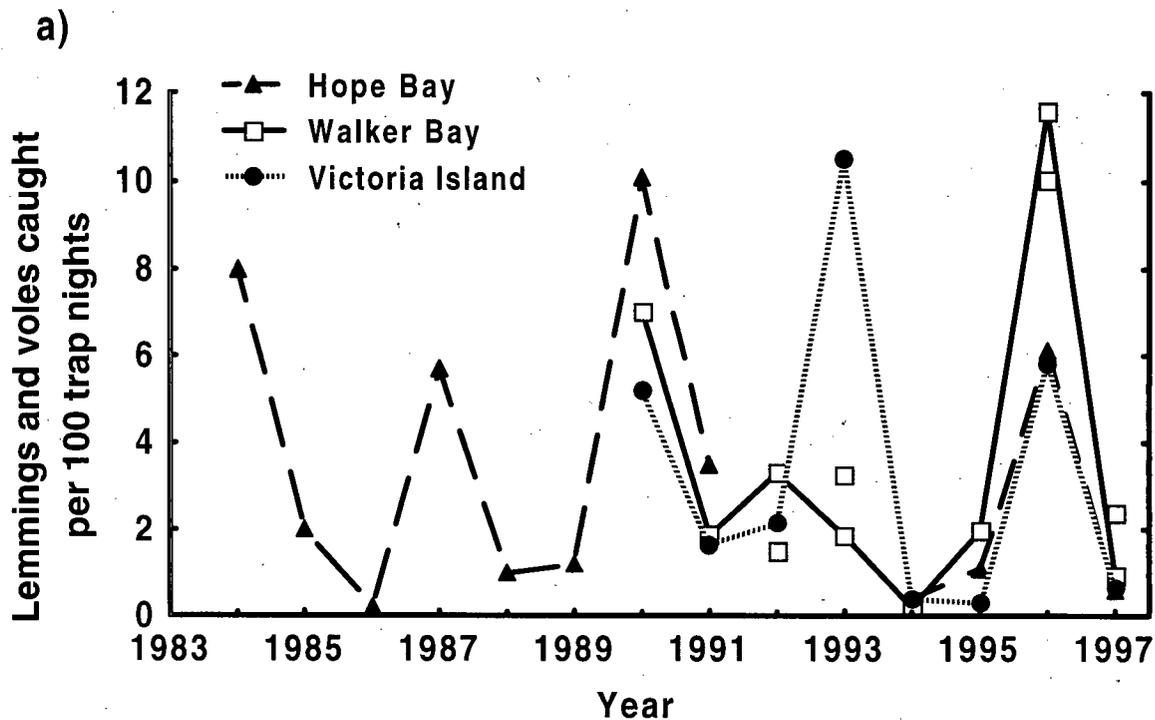
Throughout the Arctic, most populations of lemmings have cyclic dynamics, peaking in density about every three to five years (Elton 1942). On the Taymyr Peninsula in Siberia the breeding success of brent geese (*Branta bernicla*) fluctuates dramatically (Summers 1986). The number of first-year birds reaching the wintering grounds in Britain is usually highest after a summer of peak lemming (*Lemmus sibiricus* and *Dicrostonyx torquatus*) abundance, and lowest in the following year. This pattern is thought to result from predators feeding on lemmings when they are abundant but "switching" to the eggs and young of birds after lemming numbers crash (Roselaar 1979, Summers 1986). Predation on birds is expected to be particularly severe in the year after a lemming peak, if predators breed most successfully during the peak and hence increase in numbers in the subsequent year (Dhondt 1987, Summers and Underhill 1987). However, Spaans *et al.* (1998) observed that this delayed numerical response of arctic foxes did not always occur on the western Taymyr. Good breeding success in peak lemming years and poor productivity in other years has been documented in other species of Arctic-nesting geese, including lesser snow geese (*Anser caerulescens caerulescens*) on Wrangel Island (Bousfield and Syroechkovskiy 1985), greater snow geese (*A. c. atlantica*) in the eastern Canadian Arctic (Boyd 1989, Tremblay *et al.* 1997), and barnacle geese (*Branta leucopsis*) on Vaygach Island in Russia (Syroechkovskiy *et al.* 1991). Rates of nest failure in lesser snow geese at La Pérouse

Bay in northern Manitoba, however, were low and varied little among years (Cooke *et al.* 1995, p. 113).

In the central Northwest Territories of Canada, the abundance of small mammals, including collared and brown lemmings (*Dicrostonyx groenlandicus* (Traill) and *Lemmus trimucronatus* (Richardson)), has peaked every three years since 1984 (Fig. 4-1a) (Poole and Boag 1988, Cotter 1991, this study). Nest success, the fraction of nests in which at least one egg survived to hatch, of greater white-fronted geese (*Anser albifrons frontalis* Baird) and Richardson's Canada geese (*Branta canadensis hutchinsii* (Richardson)) has fluctuated widely since 1987 (Fig. 4-1b; Bromley *et al.* 1995). Nest success was synchronous between the two species and most nest failures were due to predation. However, the fluctuations in nest success were not highly synchronised with the lemming cycle. For example, during the 1987 lemming peak nest success was poor, in the 1996 peak it was good, and in 1990 and 1993 it was intermediate.

Indirect effects of lemmings on geese as a consequence of shared predators could occur through the predators' functional or numerical responses (Solomon 1949; Holling 1959a, 1961) to changes in lemming density. If predators spend less time searching and hence encounter fewer goose nests when lemmings are abundant, the predation rate on nests will tend to decrease then. If predators breed during lemming peaks and therefore increase in numbers, the predation rate on nests might increase instead. Holt (1977) called these alternatives "apparent mutualism" and "apparent competition". Theoretically, if prey types share habitat patches apparent competition should occur at equilibrium, but if prey types are in separate patches the competition will be weakened (Holt 1977, 1984). In model systems, cyclic population fluctuations also tend to weaken apparent competition because the variability in prey abundance reduces the average density of predators (Abrams *et al.* 1998). Indirect interspecific effects are usually predicted in terms of changes in equilibrium abundance, which are difficult to define and measure in

Fig. 4-1 (a) The small mammal abundance index in June (unconnected open squares) and July (connected open squares) snap-trapping at Walker Bay (this study), at Hope Bay (40 km south-east of Walker Bay) (Poole and Boag 1988, Cotter 1991, C.J. Krebs and A.J. Kenney unpubl.), and on Victoria Island (this study and C.J. Krebs and A.J. Kenney unpubl.), from 1984 to 1997. Collared and brown lemmings were caught at all three locations. Voles (*Clethrionomys rutilus* and *Microtus oeconomus*) were caught at Hope Bay only. Comparison of the June and July results from Walker Bay suggests that lemming density was increasing in 1992 and decreasing in 1993; the peak may therefore have occurred between the July trapping dates. (b) Mean nest success rates of Canada and white-fronted geese at Walker Bay from 1987 to 1997 (Bromley *et al.* 1995, this study). Error bars indicate standard errors of the mean. "P" denotes peak lemming years.



fluctuating populations. More mechanistic indicators, such as predation rate, predator effort per prey type (Abrams and Matsuda 1993), and the numerical, aggregative, and switching responses of predators may be more useful (Holt and Lawton 1994).

We tested the hypothesis that the pattern of predation on goose nests (nests lost per km²) during a three-year lemming cycle could be predicted from (1) functional responses of nest predators to lemming density, and (2) timing of the numerical response: whether predator numbers increase during the lemming peak (e.g. through aggregation) or the following year (e.g. through breeding). Nest density was much more consistent among years than was lemming density (C.V.: white-fronted goose nest density 1989 – 1994: 31; Canada goose nest density: 33; July lemming index 1990 – 1994: 97) and therefore we ignored possible responses of predators to changes in nest abundance. The primary predators on goose eggs at this location are arctic foxes (*Alopex lagopus*), glaucous gulls (*Larus hyperboreus*), and parasitic jaegers (*Stercorarius parasiticus*); all three also eat lemmings. We estimated the numerical responses of these predators by recording all sightings during the nesting periods of 4 years, 1994 – 1997, characterised by low, increasing, peak, and declining lemming abundance. We obtained indices of functional and total responses of the predators by observing them foraging in prime goose nesting areas in the summers of 1995 – 1997. Finally, we used the rate of attacks on artificial goose eggs as an index of the total response of egg predators to lemming density.

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). Annual systematic searches for goose nests are conducted over 10 – 15 km² (Bromley *et al.* 1995). Canada geese nest preferentially on islands

and the edges of ponds; white-fronted geese typically nest among hummocks away from pond edges. 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. Glaucous gulls nest colonially on islands in several lakes.

Collared lemmings are most abundant in hummocky habitats dominated by shrubs, and brown lemmings in wetter habitats dominated by grasses and sedges. Because of the fine-grained character of the study area, hummocky habitats and wet habitats are closely juxtaposed, often within a few to 50 m of each other. Thus lemmings may be abundant throughout much of the study site, and habitats of lemmings and geese overlap to a large degree. However, the distribution of goose nests was not uniform: patches (about 1 – 3 km²) with high nest densities were identifiable (Fig. 4-2).

METHODS

We assessed relative abundance of lemmings at Walker Bay annually from 1990 to 1997, and on Victoria Island from 1990 to 1994, by means of Museum Special snap-traps. We trapped in July and in some years at Walker Bay also in June. One hundred traps, baited with a mixture of peanut butter and rolled oats, were placed 10 m apart in 2 – 3 lines separated by at least 100 m and checked each morning. Trap lines crossed a mixture of habitats; when possible traps were placed near burrows or runways. Each year the number of effective trap-nights (defined as total trap-nights less misfires, lost traps and captures of non-target species) exceeded 400 at each location. We calculated an index of small mammal abundance as the number caught (excluding shrews) per 100 effective trap-nights. We did not correct for reduced trapping time per trap when catch rates of target species were high, because we assumed any such reduction was small since the highest catch was about 11 per 100 trap nights (Results). Similar surveys took place at

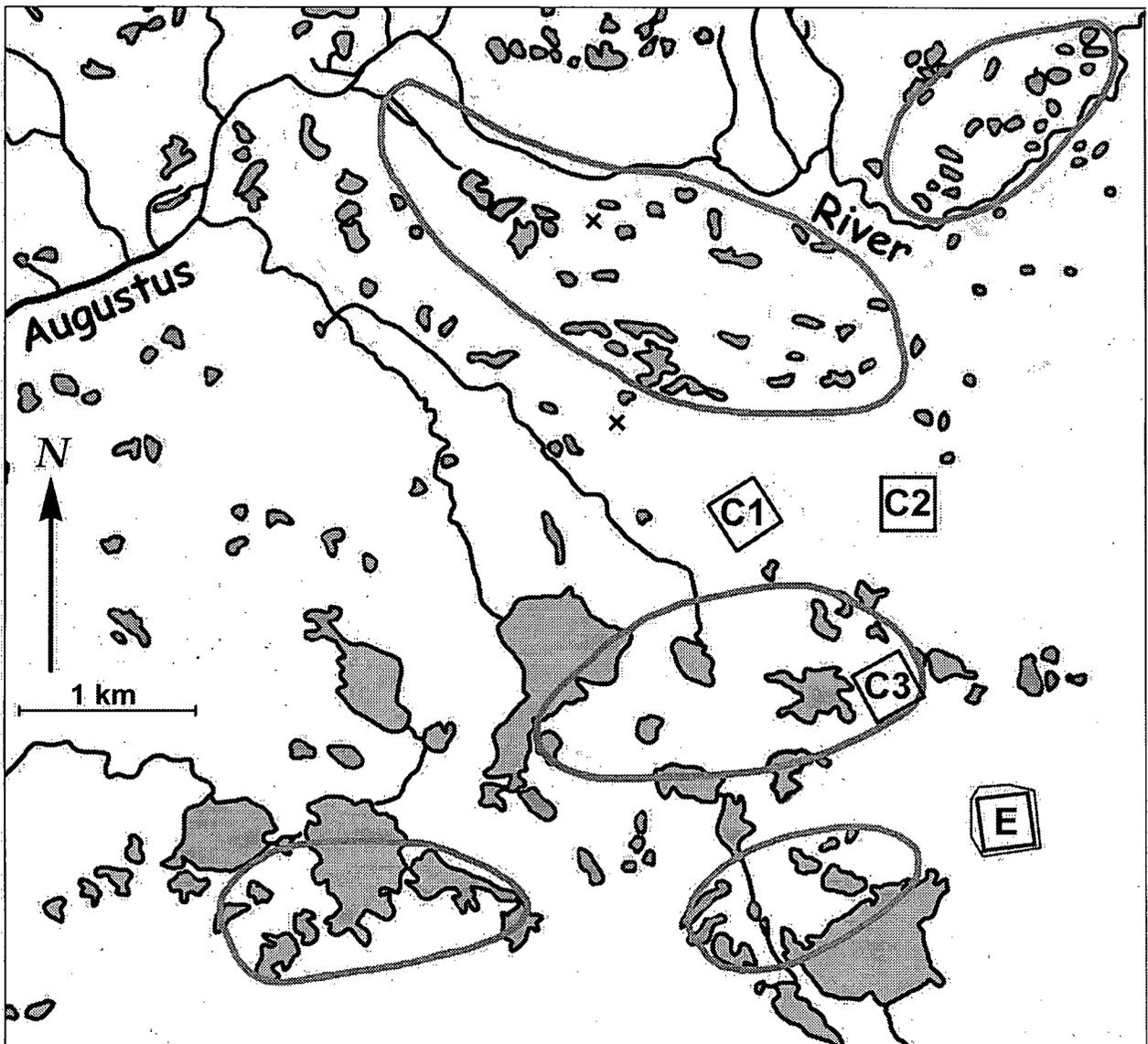


Fig. 4-2. Map showing approximate areas where geese nest at high density (grey contours) at the Walker Bay study area on the Kent Peninsula, N.W.T. The boundaries of these patches varied from year to year. Crosses (north-central area of map) represent observation towers used for predator studies in 1995 – 1997. Squares show trapping grids (9 ha) used for live-trapping lemmings, for comparison to Fig. 2-1.

Hope Bay (40 km south-east of Walker Bay) from 1984 to 1991 (Poole and Boag 1988, Cotter 1991). C. J. Krebs and A.J. Kenney (pers. comm.) have surveyed lemmings since 1995 on Victoria Island and since 1994 at Hope Bay, with slightly different protocols and over 1100 trap-nights annually at each site.

We measured the numerical responses of predators during the goose nesting period by summing all sightings per hour recorded in the field by all observers (a single datum per day). Observers travelled throughout the study area and spent less than half their time in the most intensive goose nesting areas. To represent the goose nesting period in each year we selected data from the 30 days (Bromley *et al.* 1995) beginning on the estimated first day of nesting (mean nest initiation date minus 2 SE). We could not compare the observation data among years with conventional parametric or non-parametric statistics without violating assumptions of these methods: the data contained many zeroes, their skewed distributions could not be transformed to become normal, and the distributions differed among years, violating an assumption of non-parametric tests (Conover 1980). Instead we used the bootstrap technique (Efron and Tibshirani 1993) to estimate confidence intervals of the means of the data from each year, without requiring any assumptions about probability distributions. For example, from the 30 days of fox observation data in 1996, we randomly sampled 30 values, with replacement, and calculated their mean. We repeated this procedure 5,000 times and calculated the grand mean. The 95% confidence limits were set to upper and lower percentiles of the 5,000 means. The percentiles used were not precisely the 2.5th and 97.5th, but bias-corrected and accelerated (BC_a) values (Efron and Tibshirani 1993). We inferred a significant difference between means when confidence intervals did not overlap. Because such a guideline is conservative when the size of each sample exceeds 10 (Browne 1979), in one instance we considered non-overlapping 94% confidence intervals to indicate significance, and we noted non-overlapping 90% confidence intervals also.

To observe the abundance and behaviour of predators in the prime goose nesting areas, we performed continuous scans from two observation towers, about 3 m high and 1.2 km apart. In clear weather it was possible to identify predators from a distance of 1 km; we deleted observations from the few occasions when visibility was poor. Observations were made during the nesting period from alternate towers, from 0700 to 0900 hours. This time of the morning was chosen to coincide with times when foxes, jaegers, and gulls were all active, based on preliminary trials. It is possible that predator behaviour differed at other times; for example foxes may have made more or fewer predation attempts at night when both geese and predatory birds were less active. Every 6 minutes we scanned with binoculars ($8\times$ magnification) throughout 360° . Of this time, 4.8 minutes were spent scanning (the remaining 1.2 minutes were used for recording). All sightings of predators were recorded; if the same individual was seen in two scans it was recorded again. We averaged the numbers of sightings of each species per scan over the two-hour session to create a single observation per session. We then bootstrapped means and confidence intervals for all observation sessions within each year, as above. The numbers of tower observation sessions were 16 in 1995, 18 in 1996, and 13 in 1997.

When a fox was sighted we focussed on it with binoculars or a spotting scope ($20\times$) and recorded its behaviour every 9 seconds, as one-letter codes on a pre-printed form. Scan sampling ceased during these focal observations. We recorded the following activities: travelling and searching (as defined by Stickney 1991), stopped, attacking, eating, and intraspecific and interspecific interactions. When the behaviour involved prey, we noted the prey type. Within a particular 2-hour session it was possible to distinguish individual foxes either by unique pelage, because arctic foxes moult during this period, or by location. For each fox seen on a given day, the proportion of time spent foraging was estimated as the ratio of the number of observations of foraging behaviours to the total number of observations. We defined travelling, searching, and attacking to be foraging behaviours; we initially supposed travelling not to be a foraging activity,

but it became clear that rapidly moving foxes were hunting, traversing large areas in zig-zag “transects”. Eating, which in functional response theory is considered handling time, was not considered foraging behaviour. The mean proportions of time spent foraging by foxes were compared among years by examining bootstrapped confidence intervals as described above.

The nesting success of geese, the fraction of nests in which at least one egg survived to hatch, was determined as described in Bromley *et al.* (1995). Predation was the usual proximate cause of nest failure. We also estimated the mean number of nests of each species lost per km² in 1989 – 1997 because this statistic should reflect the total response of nest predators, i.e. the product of the number of predators and the number of nests taken per predator. Precision of these means was estimated by applying the bootstrap method described above to the numbers of nests depredated in each km² searched in systematic ground searches (these were not done in 1987 or 1988), not including nests preyed upon or abandoned as a result of disturbance by humans.

We supplemented nest predation data by counting attacks on artificial goose eggs, because it can be difficult to determine the type of predator responsible for nest loss, and because a single natural egg stolen from a nest may not be recorded. We made plaster eggs in moulds and painted them with latex paint. At the beginning of the nesting period, we placed eggs uncovered on the tundra near the intersections of a 300 m × 300 m grid of 4 rows of 4 solitary eggs spaced about 100 m apart (the typical minimum distance between goose nests). We introduced variation into the grid by placing the eggs at random 10 m to the north, south, east or west of the grid points. We tethered each egg to a tent peg with 1 m of fishing line tied to a screw in the plaster. Chicken eggs were embedded in the plaster of 2 of each 16 artificial eggs in an attempt to prevent predators from learning that the eggs were inedible. We used 6 grids of 16 eggs in 1995 and 4 grids in each of 1996 and 1997. Half the grids were placed in high-density goose nesting areas, and half in low-density nesting areas. We put eggs out 3 – 4 days after the

mean date of nest initiation and checked them after 24 h to determine whether they had been attacked. Usually it was easy to identify the type of predator responsible for attacks by the marks left by its bill or teeth. Gulls made deep scratches, whereas jaegers made small paired indentations with the tips of their bills. Foxes sometimes scent-marked with urine or faeces. Each year we spent about 2 hours watching from observation towers to validate our species identifications.

We compared the number of eggs attacked per grid among years and between areas of high and low nest density with logistic regression (a generalised linear model for binomial data). We selected a parsimonious model by eliminating terms that explained little variation in the response variable according to an approximation of Akaike's information criterion (AIC) (Akaike 1974). Treatment contrasts (t-tests) were used to compare means that appeared to differ among years – the increase versus the peak phase and the increase versus the decline phase – without performing an excessive number of comparisons. Functions “glm” and “step” in S-Plus (Statistical Sciences 1995) were used for these analyses.

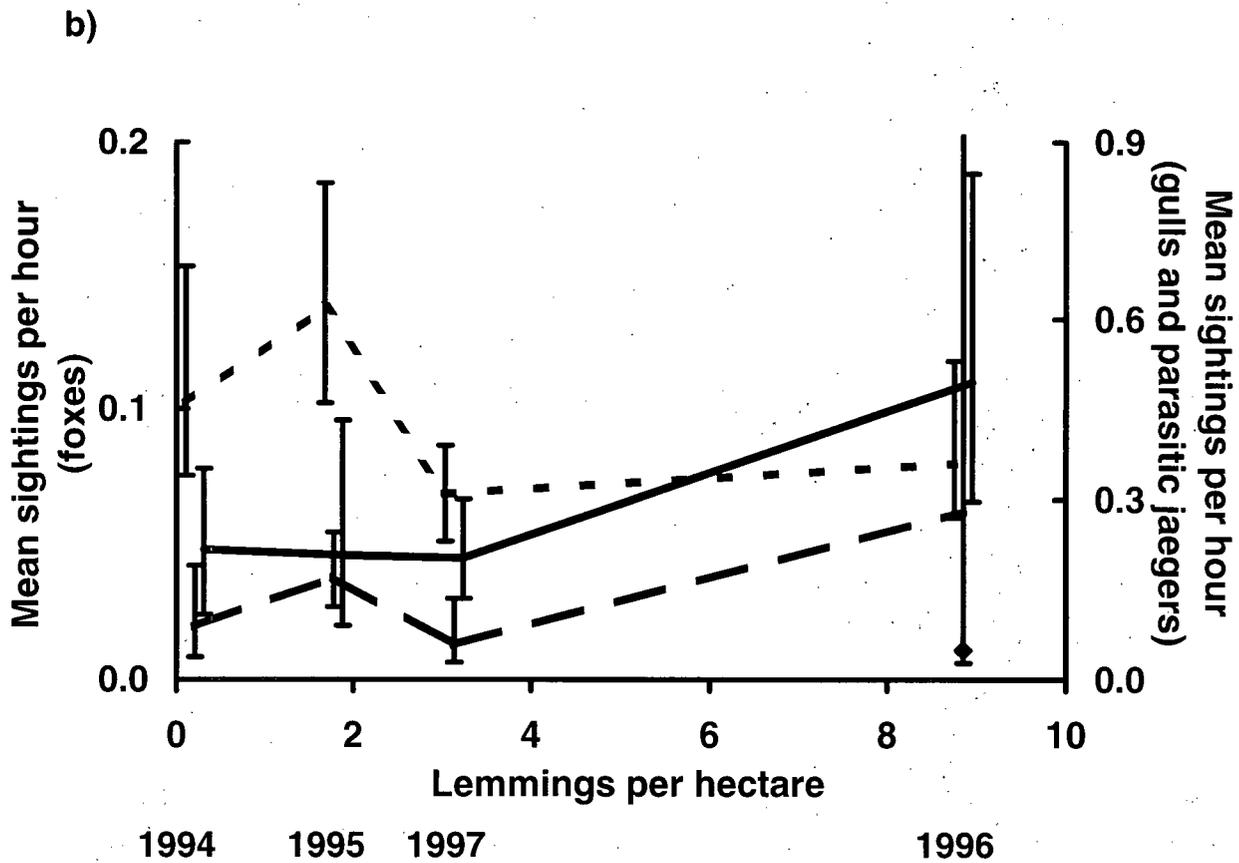
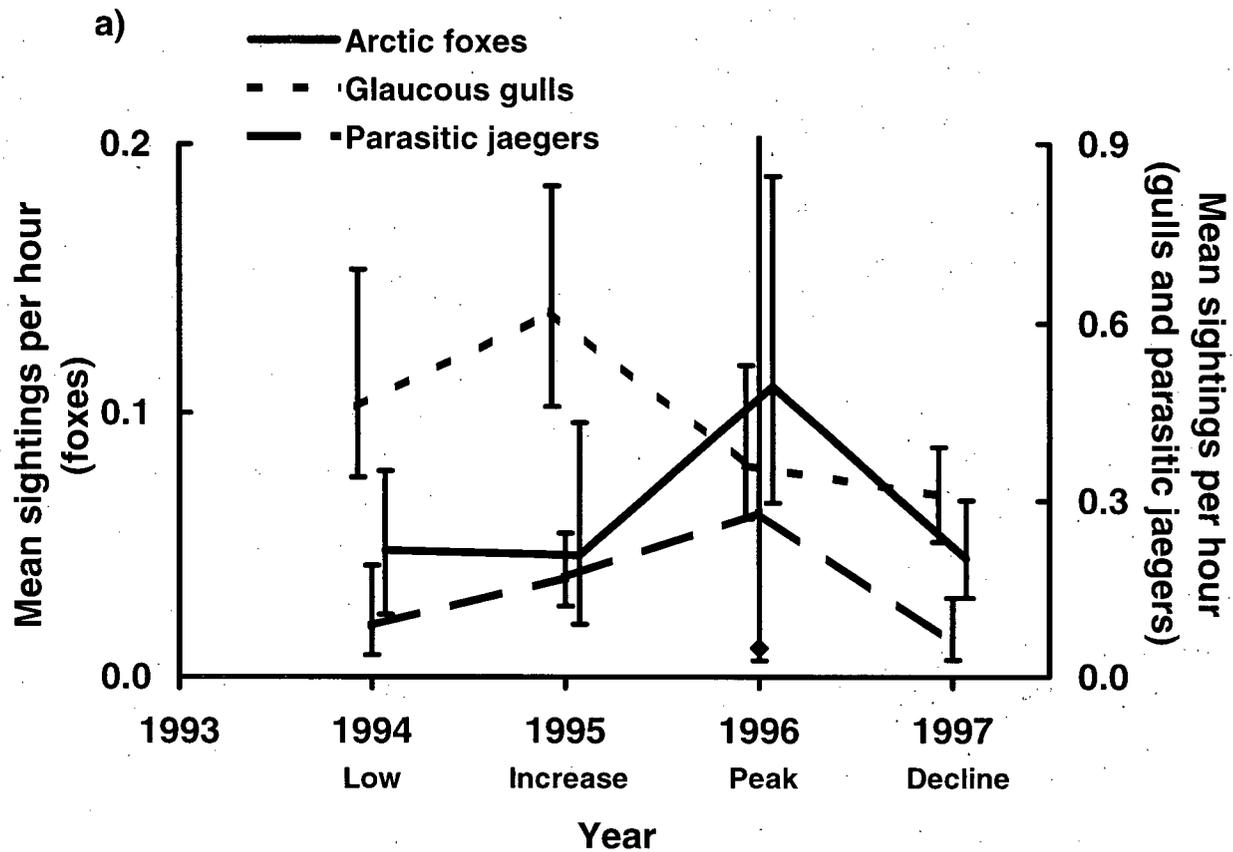
RESULTS

In 1994, numbers of lemmings were extremely low (July small mammal index at Walker Bay = 0) following a decline late in 1993 (Fig. 4-1a). Lemming density increased in 1995 (index = 1.8) and peaked in 1996 (index = 11.4). In 1997 lemming density declined during the summer: the index fell from 2.2 in June to 0.7 in July.

Numbers and foraging patterns of predators

Sightings of arctic foxes, but not of glaucous gulls or parasitic jaegers, were positively related to lemming density (Fig. 4-3). During the peak lemming year (1996), the 94%

Fig. 4-3. Mean sightings per hour of arctic foxes, glaucous gulls, and parasitic jaegers in the study area as a whole, during the goose nesting periods of 1994 through 1997, (a) relative to year (phase) of the lemming cycle, (b) relative to lemming density (mark-recapture estimates, Chapter 2). Error bars show 95% confidence intervals of the mean, calculated by bootstrapping from the data. The filled diamond shows the mean sightings of parasitic jaegers in 1996 after removal of an outlying datum of 7 seen in one hour.



confidence interval for mean hourly sightings was 0.068 – 0.183; in the following year (1997) the equivalent interval was 0.030 – 0.066. Though there were not significantly more sightings in 1996 than in 1994 or 1995, the above result emphasises the lack of a one-year delay in the increase in fox numbers. We observed more active fox dens and larger litter sizes during the lemming peak than in other years (Table 4-1a).

Sightings of glaucous gulls (Fig. 4-3) seemed to be inversely related to lemming abundance. We saw more gulls hourly during the increase than during the subsequent decline phase (95% confidence); in the peak and the preceding low phase (1994) numbers of sightings were intermediate. Sightings of parasitic jaegers followed a trend similar to gulls (90% confidence), except in the peak year. The high mean and variance in 1996 resulted from an outlying observation of 7 jaegers per hour on one day; removing this datum resulted in a mean close to that of 1997 (Fig. 4-3). There were no substantial trends in the frequency of sightings of predators over the 30 days of observations in each year.

In 4.8-minute scans from observation towers in the goose nesting area during the nesting period, we saw gulls much less often during the peak phase of the lemming cycle than during the increase phase (99% confidence, Fig. 4-4). This result confounds the number of gulls in the study area as a whole with the proportion of time each spent in the goose nesting area. Although the mean number of hourly sightings of gulls in the study area was also lower during the peak than during the increase phase (Fig. 4-3), the difference was not statistically significant (< 90% confidence). Together, these results imply that gulls spent less time foraging in the goose nesting area during the peak than during the increase phase, irrespective of their relative abundance in the two years. Pomarine jaegers (*Stercorarius pomarinus*), which are usually seen at Walker Bay only during migration, nested in wet areas of the study site at a density of approximately 2 pairs km⁻² during the lemming peak of 1996. We observed them in the goose

Table 4-1 (a) Numbers of known active dens of arctic foxes and largest observed litter sizes (one litter per active den per year) in the Walker Bay study area, Kent Peninsula, N.W.T. in 1994 through 1997, and (b) numbers of arctic fox pelts sold by the communities of Omingmaktok (Bay Chimo) (Om), Bathurst Inlet (BI), and Cambridge Bay (CB) in the preceding winters (fox pelt data courtesy of A. D'hont, Department of Resources, Wildlife and Economic Development, Government of the N.W.T.).

(a)

<u>Year (phase of lemming cycle)</u>	<u>Known active dens</u>	<u>Largest observed litter</u>
1994 (low phase)	0	—
1995 (increase phase)	5	4
1996 (peak phase)	10	11
1997 (decline phase)	0	—

(b)

<u>Winter</u>	<u>Sales of arctic fox pelts</u>		
	<u>Om</u>	<u>BI</u>	<u>CB</u>
1993 - 1994	280	47	419
1994 - 1995	267	51	469
1995 - 1996	0	0	70
1996 - 1997	149	23	597

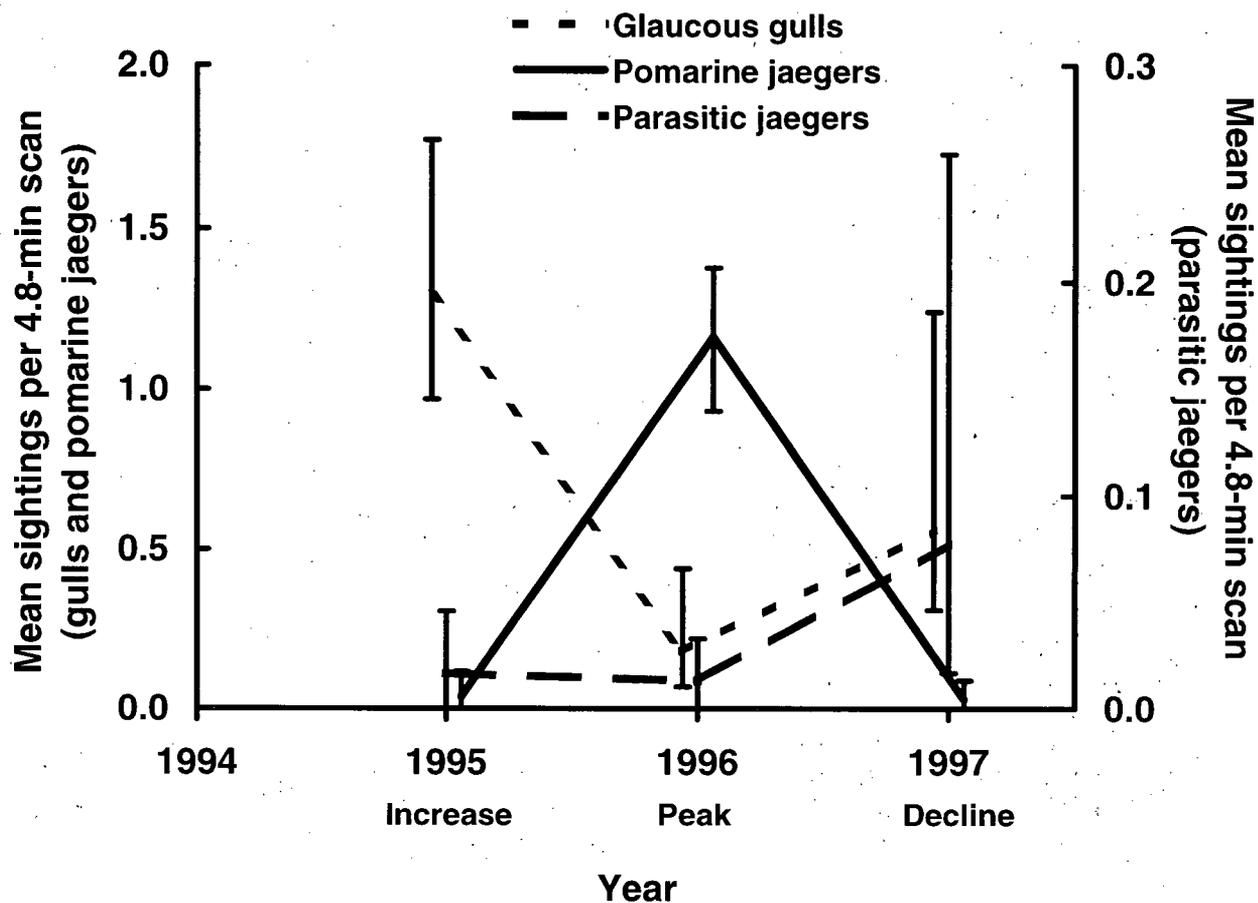


Fig. 4-4. Mean sightings per 4.8-minute scan from observation towers in the goose nesting area, of glaucous gulls, parasitic jaegers, and pomarine jaegers. Scans took place during the goose nesting periods of 1995 through 1997. Error bars show 95% confidence intervals of the mean, calculated by bootstrapping from the data.

nesting area much more often during that year than in the increase or decline years (Fig. 4-4; 99% confidence). In the first 5 days of the goose nesting period of each year we saw relatively few predators from the towers, but otherwise there were no within-year trends in our observations.

The proportion of time that foxes were seen engaging in foraging activities in the goose nesting area during the nesting period was lowest in the peak year (Fig. 4-5). Observed foxes spent 45% of their time foraging in the peak year, significantly less than the 83% of their time spent foraging in the decline (95% confidence intervals did not overlap). In the increase phase the corresponding fraction was 87%, which also approached a statistically significant difference from the 1996 value (91% confidence). We recorded a fox eating only in 1995, when one individual ate what appeared to be carrion, for almost half the total time it was observed. We saw only 4 foxes from towers during the lemming peak, although in that year we saw them more often in the study area as a whole and we spent more time scanning than in other years. Only 2 of these 4 foxes foraged; the others carried offspring or rested.

Nest predation

The numbers of goose nests depredated per km² (Fig. 4-6) appeared more synchronised between the two species than did nesting success (Fig. 4-1b). The number of goose nests of both species lost per km² were generally inversely proportional to nesting success. This relationship was not consistent in the case of Canada geese because the mean number of nests lost per km² each year was correlated with mean nest density ($r = 0.63$, $t_7 = 2.2$, $p < 0.07$). The number of white-fronted goose nests lost per km² each year was not correlated with the density of nests of white-fronted geese ($r = 0.21$, $t_7 = 0.6$, $p > 0.5$), but was correlated with the density of Canada goose nests ($r = 0.74$, $t_7 = 2.9$, $p < 0.03$) and with the total density of nests of both species ($r = 0.61$, $t_7 = 2.0$, $p < 0.09$). Nest density was less variable than lemming density, but in 1997 the

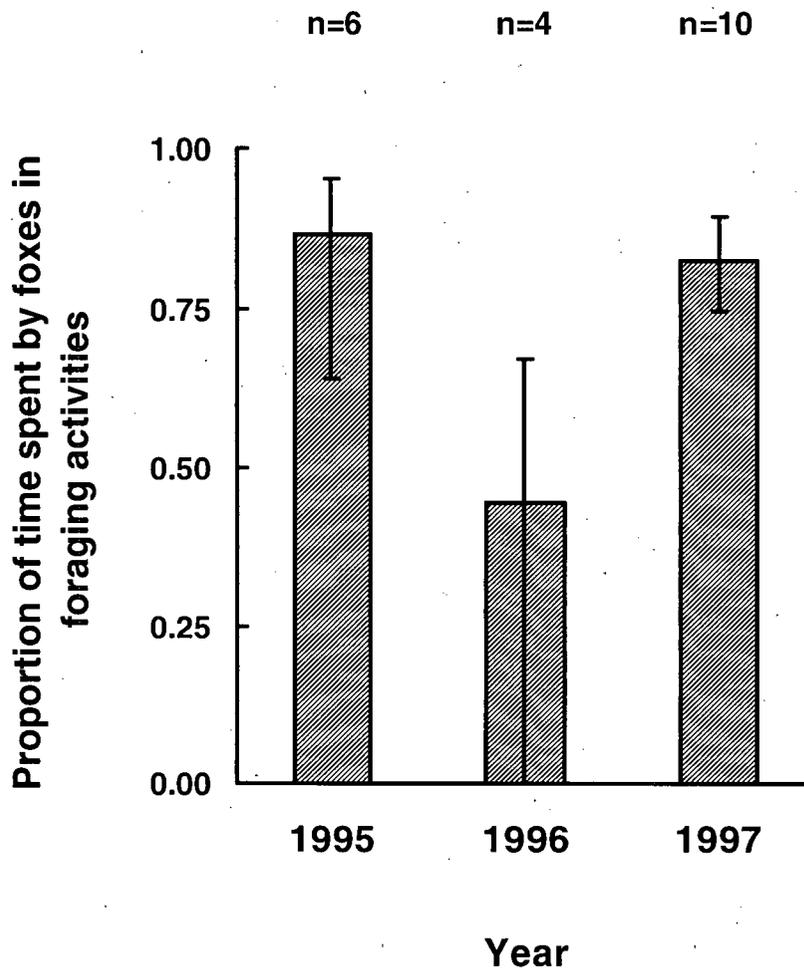


Fig. 4-5. Mean proportion of time spent in foraging activities by arctic foxes seen from observation towers in the goose nesting area, during the nesting periods of 1995 through 1997. Error bars show 95% confidence intervals of the mean, calculated by bootstrapping from the data. Sample sizes (n) refer to numbers of foxes observed.

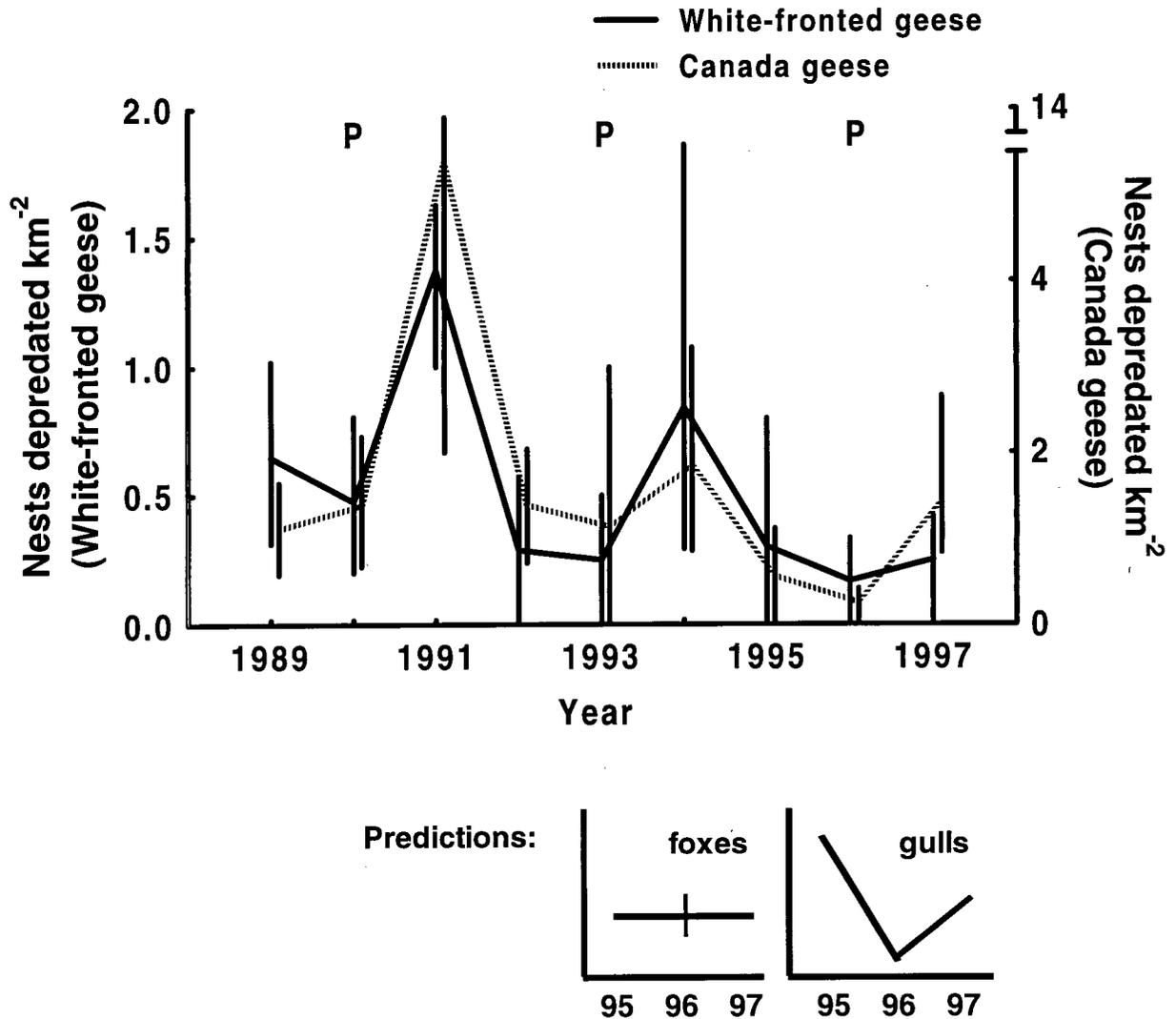


Fig. 4-6. Mean number of nests of white-fronted and Canada geese depredated per km² in 1989 through 1997, at Walker Bay on the Kent Peninsula, N.W.T. "P" indicates peak lemming years. Inset shows the patterns of nest predation predicted during 1995 (increase phase of lemming cycle), 1996 (peak), and 1997 (decline) if either gulls or foxes are the more important predator (see Discussion).

nest density of both species was unusually low (white-fronted geese 0.67 km^{-2} , 95% confidence interval $0.25 - 1.25$; Canada geese 1.75 km^{-2} , 95% C.I. $1.08 - 2.83$; cf. Bromley *et al.* 1995).

Hence the number of Canada goose nests lost was moderate relative to previous years, even though nest success was low.

Artificial eggs

A higher proportion of artificial eggs was attacked during the increase phase than during either the peak or the decline phases of the lemming cycle (Fig. 4-7) (treatment contrasts, $t_{11} > 4.4$, $p < 0.001$). Nest density explained little variation in attack rates on artificial eggs and was eliminated from the model; data from areas of high and low nest density were pooled in Fig. 4-7. In 1995, most attacks on the eggs were by gulls (Fig. 4-7). Especially in that year, gulls often attacked the same egg repeatedly, causing considerable damage that may have masked earlier attacks by other types of predators. In 1996 and 1997, most attacks were by jaegers (all species combined). Attacks (including scent-marking) by foxes were observed in 1997 only. One attack by a common raven (*Corvus corax*) was recorded in 1997. Although part of the decrease in gull attacks could have occurred because gulls became habituated to the artificial eggs after the first year, this bias is likely unimportant, since the pattern of gull attacks matched the pattern of sightings of gulls in the goose nesting area (Fig. 4-4).

DISCUSSION

Predator abundance

Peak abundance of arctic foxes may occur in the same years as lemming peaks or may be delayed by one year (Elton 1942). Arctic foxes rear larger than average litters during peak lemming years and may not breed in other years (Garrott and Eberhardt 1987, Angerbjörn *et al.*

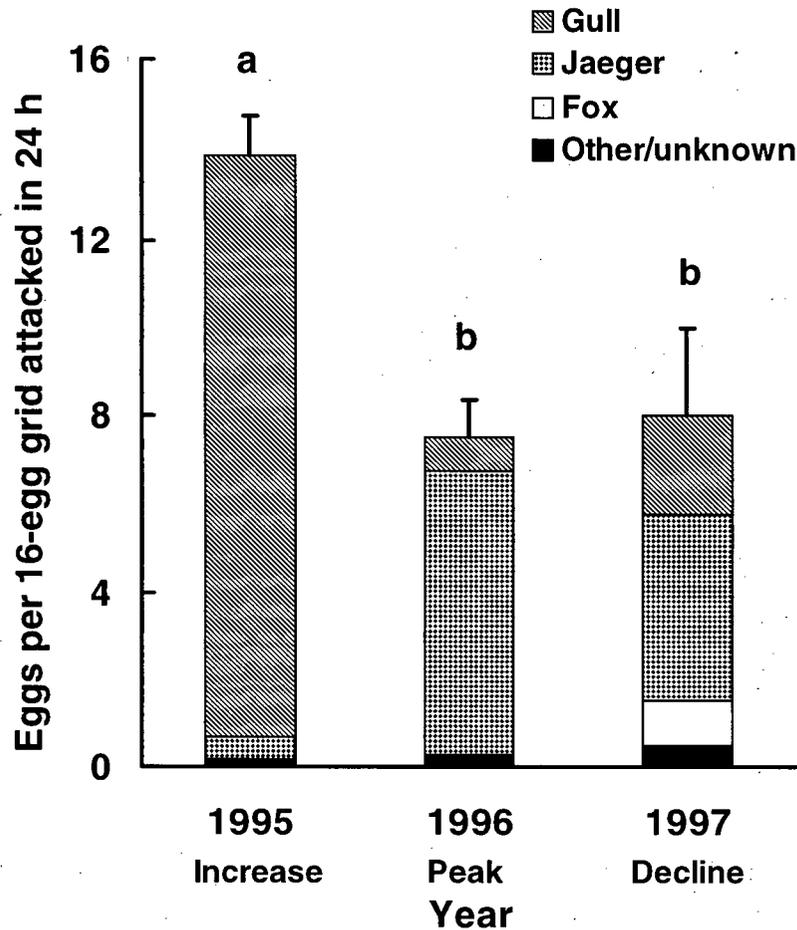


Fig. 4-7. Mean numbers of artificial goose eggs per grid of 16 eggs attacked by arctic foxes, glaucous gulls, jaegers (all species combined), and other predators within 24 hours, at the beginning of the nesting periods of 1995 through 1997. The numbers of grids were 6 in 1995 and 4 in each of 1996 and 1997. Different lower case letters denote significant differences between years in attacks by all predator types combined (treatment contrasts, $p < 0.001$). The error bars represent the standard error of the mean of the number of attacks by all predator types combined.

1995); the foxes at Walker Bay were no exception (Table 4-1a). However, although juvenile foxes hunting alone or in groups were common at Walker Bay in August and September of 1996, many had apparently emigrated or died before the following spring. Arctic foxes travel long distances (Garrott and Eberhardt 1987); some may succumb to other predators or starve when lemmings decline or become less accessible under deep snow. We found two foxes dead of unknown causes on the study area during spring 1997. Hunting by humans doubtless has an impact, as people traditionally trap on the Kent Peninsula in winter. In 1997 we found 5 fox traps left on the tundra, whereas from 1986 to 1996 we found only one or none each year. Trappers reported that 162 pelts came from the Kent Peninsula in the winter of 1996 – 1997 (G. Corey, Department of Resources, Wildlife and Economic Development, Government of the N.W.T., pers. comm.). The number of furs sold by trappers from Omingmaktok (the nearest community, 80 km to the south) in the winter following the lemming peak (1996 – 1997) was not high, but sales from Cambridge Bay that winter exceeded those in the preceding three years (Table 4-1b).

Functional responses of predators

Arctic foxes and probably glaucous gulls foraged less in the goose nesting area during the lemming peak than during the increase phase. We infer from these reductions in time directed at foraging for eggs that the number of nests taken by individual foxes and gulls declined accordingly. Such a decline demonstrates a third dimension of the functional response – decreases in the number of nests taken per predator as a function of lemming density. It is unnecessary to our purpose here to assess the probable increase in the number of lemmings eaten per predator.

The functional response by arctic foxes to lemming density likely resulted in part from habitat structure, since arctic foxes seem to prefer large eggs to small mammals. On two

occasions during the long-term nesting study from 1986 to 1997, a sandhill crane egg (*Grus canadensis*) was removed from a nest of two eggs and a lemming carcass left in its place, and once a fox temporarily dropped four dead lemmings to try to take one of the tethered artificial eggs. Stickney (1991) observed that eggs were a primary prey of arctic foxes in Alaska even when microtines were abundant. Breeding foxes remain within territories large enough to sustain them and their offspring, whereas non-breeders are not territorial and can hunt elsewhere (Bousfield and Syroechkovskiy 1985). Another interpretation of this behaviour is that if the habitat near the den is sufficiently productive in terms of lemmings, it is inefficient to travel further to search for goose eggs (the marginal value theorem, Charnov 1976). The fine-grained distribution of habitat at the Walker Bay study area meant that some goose eggs were available near dens, but breeding foxes may not have travelled to the high-density nesting areas. Similarly, the inverse numerical response by gulls may have occurred as a result of habitat patchiness. Lemmings may have been sufficiently abundant during the peak for gulls to forage near their own nests, not hunt further afield, and therefore be observed less often. The same thing may have occurred during the decline in 1997. Lemming density may have been quite high early in spring 1997. In a concurrent live-trapping study, mean lemming density in June 1997 was higher than in June 1995, and since density was declining in 1997, it may have been even higher in May 1997 (Chapter 2). In late May and early June 1997, we often saw snowy owls (*Nyctea scandiaca*) and short-eared owls (*Asio flammeus*) and found owl pellets containing lemming remains. Sightings of parasitic jaegers may have been affected in this way (Fig. 4-3), but we have too few observations to be able to draw conclusions about their foraging effort (Fig. 4-4).

Changes in foraging behaviour could be examples of prey switching, which can be thought of as a change in the preferences of the predator (Murdoch 1969). Switching is recognised when the proportion of a prey type in the predator's diet is an increasing function of

the density of that prey, within a range of prey densities (Murdoch 1969). Alternatively, switching may be thought of as an increase in the rate of effective search for one prey relative to another, as the ratio of the densities of the two prey types increases (Murdoch 1973). This model often (but not always) leads to a sigmoid (Type III, Holling 1959a) functional response curve (Murdoch 1973). However, we have not estimated most of these relationships. A Type II curve fitted the data of numbers of lemmings consumed by arctic foxes as a function of lemming density better than did a Type III curve (Chapter 3), but there were few data at low lemming density. Switching is not necessary for apparent mutualism to occur, as long as one prey type is substituted for another in proportion to their abundance (Noy-Meir 1981).

Loss of goose nests

If we were correct in predicting that the number of goose nests depredated depends on the numerical and functional responses of nest predators to lemming density, then the pattern of nest predation (nests lost per km², Fig. 4-6) should match the total response, i.e. the pattern of the products of the observed responses of predators. Although both arctic foxes and glaucous gulls showed strong to moderate functional responses to lemming density, their numerical responses differed greatly. The inset in Fig. 4-6 shows predictions of how the number of nests taken by foxes and gulls were expected to vary in 1995, 1996, and 1997. We developed the prediction for foxes by graphically multiplying their numerical response (inferred from Fig. 4-3) by their functional response (inferred from Fig. 4-5); the vertical line indicates the considerable uncertainty in the peak year (Figs. 4-3, 4-5). The prediction for gulls was taken from the total response, inferred from the pattern of gull sightings in the goose nesting area (Fig. 4-4). The predicted pattern of nest predation depends on the relative importance of the two predators. If foxes were the only predators on goose nests there should be less predictable variation in the number of nests depredated because their functional and undelayed numerical responses would

tend to cancel each other (Fig. 4-6, inset) although they are unlikely to do so entirely. If gulls are important predators the number of depredated nests should be inversely related to the abundance of lemmings (Fig. 4-6, inset). Combining the effects of both predators averaged over many cycles, nest loss should be lowest during lemming peaks but should not differ consistently between increase and decline years.

In the case of Canada geese, the fewest nests were lost in the peak lemming year (1996), as predicted for predation by gulls or by both types of predator. Contrary to our prediction, more nests per km² on average were lost in the decline (1997) than in the increase phase (1995) but these estimates were not significantly different. The numbers of depredated nests of white-fronted geese were relatively invariant but were also lowest in the peak year, as predicted for predation by foxes or by both types of predator. Indeed, field observations indicate that the highly traditional and relatively visible nests of Canada geese are preyed on more often by avian predators than are the cryptic nests of white-fronted geese, which are used for one season only and are preyed on more often by foxes. However, because destroyed nests of white-fronted geese are difficult for biologists to find, we may have underestimated the numbers taken early in the season (Bromley *et al.* 1995). The pattern of attacks on artificial eggs was similar to that of nest loss predicted for predation by gulls. It is not surprising that gulls and jaegers were most often responsible for attacking artificial eggs, since these eggs were highly visible from the air and lacked the scent associated with geese and their nests.

Our prediction that the number of goose nests depredated should be a function of the numerical and functional responses of nest predators to lemming density was met during the years in which the responses were studied. This model would be of most use if it could be extended to other years. But data from previous 3-year lemming cycles at this location do not meet our prediction that during lemming peaks (1990, 1993) the number of nests lost should be lowest (Fig. 4-6). Instead, nest loss has tended to be greatest in the years following peaks (1991,

1994) with little variation among increase and peak years. Predators' numerical and functional responses probably vary among cycles; even the suite of predators in the system varies. For example, we observed an aggregative response to the lemming peak by breeding pomarine jaegers (Fig. 4-4), a well-known phenomenon (Maher 1970, 1974), but a response of such magnitude occurred only once in 11 years at Walker Bay. Pomarine jaegers depend more on small mammals and less on eggs than do parasitic jaegers (Maher 1974). In 1996, they were repeatedly observed aggressively defending their nests against foxes, gulls and other jaegers; in some instances the gulls and other jaegers were attempting to depredate goose nests within the territories of the pomarine jaegers once humans had disturbed the geese. In some Arctic regions, snowy owls nesting during lemming peaks protect the nearby nests of geese from other predators (Bousfield & Syroechkovskiy 1985, Tremblay *et al.* 1997), but at Walker Bay nesting snowy owls are uncommon.

The seasonal timing of the decline in lemming density is another likely source of variation in the abundance of predators. For example, if the decline occurs late in the peak year fewer foxes may survive or remain throughout the winter, and in the following spring migrating avian predators will be less likely to stop. Of course, a host of weather-related effects will introduce variation. Nest density has not varied much in most years, but in 1997 few nests were initiated because of persistent cold weather and delayed snowmelt. Predators may have responded functionally to the large reduction in the number of goose nests, taking fewer nests. We found positive correlations between nest density and the number of depredated goose nests, but observed a high rate of predation on Canada goose nests when nest density was low in 1997. When predators have a Type II functional response to prey (nest) density, the rate of predation is predicted to rise as density falls unless predator numbers drop sharply (Holling 1959a)

If the numerical and functional responses of predators vary among 3-year lemming cycles, then the phase of the cycle is not sufficient to predict the loss of goose nests. However,

in addition to fox trapping, the factors discussed above – abundant breeding pomarine jaegers, the timing of the lemming decline, and the density of goose nests – are all variables that are expected to alter the numerical and functional responses of predators. Measuring these variables may allow more accurate prediction of future relative nest loss in the increase, decline, and peak phases of the cycle on the Kent Peninsula (Table 4-2).

This system seems less predictable than that on the Taymyr Peninsula, where arctic foxes and parasitic jaegers are present, but the Taymyr gull (*Larus argentatus taimyrensis*) replaces the glaucous gull. However, it is important to recognise that the long-term data indicating breeding success in brent geese (Summers 1986) reflect not only nest success but also survival of goslings and migrating birds; hence variation in these individual components may be masked. For example, post-fledging survival of lesser snow geese at La Pérouse Bay varied greatly, apparently owing to natural mortality (not to hunting), whereas nest success varied little (Cooke *et al.* 1995, p. 115). Recently, in 6 years (2 lemming cycles) of field research on the western Taymyr, Spaans *et al.* (1998) identified several factors that interacted to affect the breeding success of brent geese. In that region, most geese bred on offshore islands, where no nest predation was recorded because in most years foxes did not visit the islands. However, in the year after one lemming peak, few nests were initiated even on the islands, apparently because of frequent disturbance by abundant foxes. In the year after a second lemming peak, few foxes were seen even on the mainland; some had been trapped and it appeared others had died of starvation. In that year, nest success was high but gulls killed most goslings. Differences in habitat structure and geography between the Kent and Taymyr Peninsulas, together with rates of fox trapping, may contribute to differences in numerical responses of predators in the two locations.

This study supports the hypothesis that nesting success of geese at Walker Bay was affected by abundance of lemmings through the functional and numerical responses of nest

Table 4-2. Testable predictions showing how factors discussed in the text should affect winter survival of arctic foxes, spring abundance of avian predators, and hence the relative number of goose nests depredated per km² on the Kent Peninsula, N.W.T. Table entries show predictions for the nesting period (spring) of the increase, peak, and decline phases of the lemming cycle.

	<u>Winter survival of arctic foxes</u>	<u>Avian predators</u>	<u>Loss of goose nests per km²</u>		
			<u>Increase</u>	<u>Peak</u>	<u>Decline</u>
Abundant breeding pomarine jaegers during lemming peak				Low	
Timing of lemming decline:					
Preceding summer or fall	Poor	Few			Low
Spring	Good	Many			High
Fox trapping in winter after peak:					
Many trapped	Poor				Low
Few trapped	Good				High
Low density of goose nests			Low	Low	Low

predators, during the 3-year cycle studied. Arctic foxes and glaucous gulls, foraging in a patchy environment, exhibited strong functional responses. Gulls showed no numerical response (or an inverse one) resulting in an apparent mutualism between geese and lemmings. A numerical response of foxes occurred during the peak lemming year only, which may have cancelled out the functional response leading to little net effect on nest predation. Better winter survival of foxes after a lemming peak might lead to apparent competition: heavier losses of goose nests in the subsequent year. Because the functional and numerical responses of predators are likely to vary among 3-year lemming cycles, these indirect effects cannot be predicted from the phase of the lemming cycle alone. Instead we have made testable predictions of how variation in the abundance of pomarine jaegers, the timing of the lemming cycle, the trapping of arctic foxes, and the density of goose nests are expected to affect the relative number of goose nests lost during the lemming cycle.

CHAPTER FIVE

CONCLUSIONS

In this thesis I tested three main hypotheses: (1) predation is necessary to limit the lemming population during the peak and decline phases of the cycle, (2) predation is a necessary cause of the decline of the lemming population, (3) the pattern of predation on goose nests (nests lost per km²) during a three-year lemming cycle can be predicted from functional responses of nest predators to lemming density, and timing of numerical responses.

Limitation of a population

Different ecologists have used the term "limitation" to describe different phenomena. In this thesis I have applied Sinclair's (1989) definition, which referred to equilibrium population density, to fluctuating populations. Hence, a limiting factor is any factor that alters the density of the population by changing production or losses. For example, predation is a limiting factor during a time period if it lowers population density during that period; it may not do so if other production or loss factors are compensatory. Recognising limitation by some factor relies on detecting a difference in density between populations with that factor present and those without. This usage of the term limitation is gaining currency (e.g. Krebs 1995).

Necessary and sufficient conditions

The terms "necessary" and "sufficient" lend precision to descriptions of causes, but can be difficult to understand. A necessary condition is a prerequisite; it must be present for the indicated effect to occur. Hence a test of necessity is that when the condition is not present, the effect must not occur, other things being equal (Chitty 1996, p. 53). If predation is necessary to

limit population density to a certain level, then without predation the population will not be limited; that is, its numbers will be higher than when predation is present. In the language of logic, this statement can be written $P' \rightarrow L'$, which is read "if not P then not L", where the symbol ' denotes "not", and P symbolises predation and L limitation. This logical proposition describes one prediction of a predator reduction experiment (Krebs 1996).

A sufficient condition is one that assures that an effect will occur. Sufficiency can be refuted if when the condition is present, the effect does not occur, other things being equal (Chitty 1996, p. 53). Therefore, if predation is sufficient to limit density by a specific amount, then density will not rise by an equivalent amount in the presence of predation. This proposition is written $P \rightarrow L$, which is logically equivalent to $L' \rightarrow P'$. These statements imply that no other experimental manipulation will result in an increase in population density equivalent to that of predator removal. Obviously, a sufficient condition is difficult to test, and I did not directly test the effects of factors other than predation on population density. Instead, I used the presence or absence of compensatory mortality to infer that other mortality factors might or might not also have been limiting in different phases of the cycle (Chapter 2). In the same way, I considered that the lower proportion of reproductive lemmings in the peak phase implied that food, space, or social factors might also have been limiting at that time (Chapter 2); therefore, predation may not have been a sufficient limiting factor during the peak.

If one factor is both necessary and sufficient for an event to occur, that event has a single cause. However, events can have multiple causes, all sufficient or all necessary (Hilborn and Stearns 1982). As well, a specific combination of antecedents might be both necessary and sufficient for a phenomenon to occur (Krebs 1996). In order to untangle multiple causes, it is important to design research carefully and to clarify with precision the hypotheses tested.

Conclusions of this thesis

1) Predation was necessary to limit the lemming population in summer of the peak and decline

I tested five predictions of the hypothesis that predation is necessary to limit the lemming population: (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.

All five predictions were met during the summer decline phase of the cycle. In the summer of the peak phase, the first, second, and fifth predictions were met. However, survival in the peak was not consistently higher within the predator enclosure than elsewhere. In addition, other unidentified sources of mortality apparently sometimes compensated for the reduced predation on telemetered animals. Still, the increase in survival was apparently enough to lead to greater density in the Enclosure. Therefore, I conclude that predation was necessary to limit density during both the peak and decline summers. However, the magnitude of the limitation was less during the peak than during the decline; this was evident in the relative differences in density observed between treatments (10-fold in the decline but only 2-fold in the peak). Predation may limit lemming density only until density rises to a level at which another factor becomes limiting.

2) Predation did not seem to be necessary to initiate the population decline, but was necessary to accelerate and continue the decline in the following summer

I tested three predictions of the hypothesis that predation is a necessary cause of the lemming population decline: (1) the lemming population should not decline in an area protected from predation when it declines on unprotected sites, (2) the predation rate on lemmings is

delayed density-dependent, and (3) the population decline is associated with an increase in predation rate.

None of the three predictions were met in autumn or winter when the decline began. Instead, the decline seems to have been initiated by cessation of reproduction by the end of July in the peak summer, implying that predation was not a sufficient cause of the winter decline. But because the predator exclosure was less effective in winter, I cannot with certainty refute the hypothesis that predation was a necessary cause of the winter decline. The contribution of predation to the winter decline depends on the extent to which causes of winter mortality were compensatory. In contrast, all three predictions were met in the following summer, when the decline accelerated. I conclude that the decline was initiated late in the peak summer by cessation of reproduction, but that a high rate of predation, primarily by ermine, was necessary to accelerate and extend the decline in the following summer.

3) The indirect effects of lemming abundance on loss of goose nests cannot be predicted from the phase of the lemming cycle alone.

I tested the hypothesis that the relative number of goose nests lost per km² during a three-year lemming cycle on the Kent Peninsula could be predicted from functional and numerical responses of nest predators to lemming density. This hypothesis was supported during the years in which I recorded the predators' responses. However, data from previous three-year lemming cycles at this location did not meet my prediction that the number of nests depredated should be lowest during lemming peaks. Instead, nest loss tended to be greatest in the years following peaks with little variation among increase and peak years. I conclude that because predators' functional and numerical responses are likely to vary among cycles, their effects on geese cannot be predicted from the phase of the lemming cycle alone. Instead, I propose testable predictions of how the abundance of pomarine jaegers, the timing of the lemming cycle, the trapping of

arctic foxes, and the density of goose nests should affect the relative number of goose nests depredated during the lemming cycle.

What causes population cycles in lemmings?

The rapid increase in numbers of collared lemmings at Walker Bay is easy to explain if their reproductive rate is high at all times except during the peak summer and the subsequent winter. Predation may limit population density to a varying degree throughout the cycle. The cessation of reproduction early in the peak summer, apparently an intrinsic response to the presence of conspecifics, initiated the decline. Assuming breeding did not recommence until March – April, the winter mortality rate was low. Hence, predation may not have been a necessary factor in the winter population decline. On the other hand, it is possible that competition for food and space in autumn and winter led to higher mortality than occurred in summer. Predation, primarily by ermine, accelerated and extended the decline in the following summer. Therefore, the deaths of ermine once the lemming population reached very low density would allow the population to grow again. I have seen no evidence of an extended low phase in this population of lemmings.

What should be done next?

Of the factors in the preceding paragraph hypothesised to explain lemming cycles, I tested only those related to predation and to summer reproduction. My conclusions about predation were weakened by imperfections in the predator enclosure and by its lack of replication. I recommend the following further research:

- 1) My study should be repeated with a replicated predator reduction treatment. Predator enclosures should have higher fences (at least 1.7 m) of doubled chicken wire to exclude arctic foxes in summer. These structures will be permeable to ermine, but summer predation

by ermine was light except in the decline, and removing ermine seemed a satisfactory solution.

- 2) Winter reproduction in collared and brown lemmings has been studied directly only in Siberia (Chernyavski 1979) and to a small extent in Canada (Krebs 1964a). The hypothesis that winter reproduction occurs in all years except at peak density needs to be tested, by trapping in autumn and winter. This project would be logistically challenging, but might be facilitated by involving people living in the north.
- 3) What shortens the breeding season in the peak summer is unknown. The social structure and relatedness of lemmings should be studied and compared among phases of the cycle. Useful methods include radio-telemetry and tagging young in nests or nest boxes, as Lambin (1993) has done with voles, and DNA fingerprinting. Our knowledge will increase fastest if we do experimental manipulations: for example, testing effects on the maturation of juveniles of (1) removing parents as Wolff (1992) did with mice, and (2) artificially enhancing density by reducing predation.
- 4) Autumn mortality of lemmings, in the peak phase before the snow is deep, should be assessed with radio-telemetry. It seems likely that the mortality rate increases in autumn owing to deteriorating weather and competition for food and space, but it is difficult to assess the condition of lemmings and to quantify food availability in the patchy tundra environment. Even data comparing mortality between August and September might be highly informative.

APPENDIX 1

ESTIMATION OF LEMMING CONSUMPTION BY ARCTIC FOXES

Determining the prey composition of arctic fox scats

My method of analysis of scat composition generally followed that of Reid *et al.* (1997) except that I focussed on lemmings in the diet rather than on the entire diet. I autoclaved the scats, dried them at 50°C for 24 hours, and weighed each to the nearest 0.01 g. I soaked each scat in water for 24 h, broke it up, and washed it over a 500 µm sieve. I discarded the particles that passed through the sieve. Discarding this microscopic fraction can lead to a slight underestimation of birds ingested, because fragments of feathers may be lost; and in temperate regions the microscopic particles can be used to estimate earthworm consumption (Reynolds and Aebischer 1991). I ignored the microscopic fraction because (1) my primary interest was in mammals in the diet, (2) earthworms do not occur in the Arctic, and (3) in preliminary examinations, the particles were composed of fine organic and mineral material, with no identifiable fragments.

I sorted the macroscopic material by species or type (bones, teeth, eggshell, large feathers, insect parts, vegetation), leaving the "remainder", which usually consisted of mammalian hair, sometimes mixed with small feathers, particles of soft tissue, vegetation, and inorganic matter (e.g. sand). I identified the remains to species, by means of mammalian teeth, bones, and hair, or to class (birds, insects). I used diagrams of microtine teeth in Banfield (1974, p. 182) and museum specimens for reference. I did not identify the species of mammals or birds by microscopic examination of hair or feathers as described by Day (1966) and Kennedy and Carbyn (1981), except to distinguish fur of arctic hare and arctic fox. I measured the length of all lemming ulnas and molar tooth rows. I estimated the percentage weight composition of the

“remainder” (hair, small feathers, soft tissue, small pieces of vegetation, sand etc.) by eye, taking into account different densities. I dried and weighed the separated fractions. I apportioned the mass of lemming hair between species of microtines based on the proportion of molars of each species (Reid *et al.* 1997). When both ground squirrel and lemming remains were present in a scat, I apportioned the mass of hair according to the mass of bones and teeth of each species. If no teeth were available for species identification, I determined the species of lemmings by the morphology of their forefeet (Banfield 1974, pp. 185, 194), which were often well preserved, or by hair colour (although hair was often very discoloured). This method usually required an assumption that only one species of lemming was present. It was possible to determine the species of lemming remains in all but 17 of 251 scats.

Estimation of biomass ingested by foxes

To estimate the ingested biomass of lemmings that would yield the observed macroscopic biomass of lemming egested per scat, I multiplied by a conversion factor of 28, which was chosen by Reid *et al.* (1997) based on lower estimates for digestion of voles by red foxes (*Vulpes vulpes*) (Lockie 1959, Goszczynski 1974). Reid *et al.* (1997) found that this value yielded estimates of lemming biomass ingested by red foxes similar to those based on the mass of undigested lemming hair.

I roughly estimated the total biomass per scat of all species ingested, in order to identify periods when the food intake of the foxes was high or low. For these conversions I classified birds as large (anseriform, galliform) or small (passeriform, charadriiform) based on feather and bone size. I used conversion factors from Reid *et al.* (1997) for red fox digestion, based on those developed by Lockie (1959), Goszczynski (1974), and Reynolds and Aebischer (1991) to convert the biomass of voles (23), ground squirrels (43, conversion factor for rabbit in Lockie), arctic hare and arctic fox (50, conversion factor for lagomorphs in Goszczynski), large (61) and small

(45) birds, caribou (100), and eggshell (9.1). I used the figure for beetles (12.4) in Reynolds and Aebischer (1991) to convert invertebrate remains. For unidentified bones I chose a conversion factor based on the size of the bones (e.g. squirrel-like). A few scats had large amounts of soft tissue with no associated bones; I used an intermediate conversion rate of 45 for this tissue as if it was ground squirrel, possibly an underestimate. I did not convert shrew remains because they occurred in trace amounts in only two scats.

Estimation of daily consumption of biomass

Red foxes defecate, on average, about 7 times day⁻¹ when well-fed (determined from snow-tracking; P.-O. Palm, pers. comm. to Reid *et al.* 1997). This estimate may be too high for arctic foxes since one can follow their tracks for many kilometres without finding a scat (K. Frafjord, pers. comm.). Captive arctic foxes eating a fixed daily amount of commercial food high in carbohydrate produced very roughly 10 scats day⁻¹ (Ø. Ahlstrøm and E. Fuglei, pers. comm.), but arctic foxes eating meat would produce fewer scats. I assumed a defecation rate of 5 scats day⁻¹ when foxes were well fed. Following the method of Reid *et al.* (1997), in periods when lack of breeding or low estimates of biomass intake per scat indicated that the foxes were poorly fed, I used lower defecation rates of 4 day⁻¹ or 3 day⁻¹ (see Results).

Estimation of daily consumption of *Dicrostonyx*

I applied the regression equations in Reid *et al.* (1997) to the lengths of ulnas and upper and lower molar rows in scats to estimate the mass of individual *Dicrostonyx* in the scats. From this I calculated the ratio of adult (> 40 g) to juvenile (≤ 40 g) *Dicrostonyx* consumed during each sampling period. Sample sizes were large enough to do this only in the summer of 1996 and in early 1997. For each of these periods I divided the proportion of adults in scats by the proportion trapped to indicate the reduced vulnerability to fox predation of adult lemmings

relative to juvenile lemmings. I estimated a correction factor to account for this reduced vulnerability in all sampling periods, as the mean of these fractions. I then adjusted the ratio of adults to subadults killed by foxes by multiplying the proportion of adults caught in each period by this factor. I then estimated the total number of *Dicrostonyx* eaten based on the biomass consumed, these ratios, and the mean mass of adults and juveniles trapped during the period.

APPENDIX 2

ESTIMATION OF LEMMING CONSUMPTION BY BIRDS OF PREY

Determining the prey composition of avian pellets

I dried each pellet at 50°C for 24 hours. I separated the pellets with forceps, sorting the hard material by species or type (bones, teeth, eggshell, large feathers, insect parts, vegetation), leaving mammalian hair sometimes mixed with small feathers. As with fox scats (above) I identified mammal remains to species by means of their teeth, feet, and hair, but did not identify the species of bird or invertebrate remains. I was able to identify the species of all lemming remains in pellets. As each of a lemming's 12 molar teeth (3 upper and 3 lower on each side) is unique, I counted and identified the species and position in the jaw of all lemming molars. I recorded the minimum number of lemmings contained in a pellet based on the number of unique molar teeth (Reid *et al.* 1997).

To estimate the number of lemmings ingested per rough-legged hawk pellet and per day, I used the conversion factors obtained from a feeding experiment by Reid *et al.* (1997). They found that the number of lemmings ingested by a rough-legged hawk exceeded the number identified in pellets according to unique molar teeth, by a factor of 1.02 when the hawk was well fed and by 1.27 when it was slightly food-stressed. A well-fed hawk produced 1.1 pellets day⁻¹ and a food-stressed hawk produced 0.9. I did not apply a conversion factor to owl digestion, because they digest less bone than hawks do (Craighead and Craighead 1956) and short-eared owl pellets closely reflected the number of voles eaten when skulls were used as an index (Lockie 1955). I assumed a casting rate of 1.55 pellets day⁻¹ for well-fed snowy owls, based on values published for other owl species (details in Results).

LITERATURE CITED

- Abrams, P.A. and Matsuda, H. 1993. Effects of adaptive predatory and anti-predator behaviour in a two-prey-one-predator system. *Evol. Ecol.* 7: 312-326.
- Abrams, P.A., Holt, R.D., and Roth, J.D. 1998. Apparent competition or apparent mutualism? Shared predation when populations cycle. *Ecology* 79: 201-212.
- Agrell, J., Erlinge, S., Nelson, J., and Sandell, M. 1992. Body weight and population dynamics: cyclic demography in a noncyclic population of the field vole (*Microtus agrestis*). *Can. J. Zool.* 70: 494-501.
- Agrell, J., Erlinge, S., Nelson, J., Nilsson, C., and Persson, I. 1995. Delayed density-dependence in a small rodent population. *Proc. R. Soc. Lond. B* 262: 65-70.
- Akaike, H. 1974. A new look at statistical model identification. *IEEE transactions on automatic control* AU-19: 716-722.
- Angerbjörn, A., Tannerfeldt, M., Bjärvall, A., Ericson, M., From, J., and Norén, E. 1995. Dynamics of the arctic fox population in Sweden. *Ann. Zool. Fennici* 32: 55-68.
- Anthony, R.M. 1997. Home ranges and movements of arctic fox (*Alopex lagopus*) in Western Alaska. *Arctic* 50: 147-157.
- Banfield, A.W.F. 1974. The mammals of Canada. University of Toronto Press, Toronto.
- Batzli, G.O. 1985. The role of nutrition in population cycles of microtine rodents. *Acta Zool. Fenn.* 173: 13-17.
- Batzli, G.O. 1992. Dynamics of small mammal populations: a review. In: McCullough, D.R. and Barrett, R.H. (eds.). *Wildlife 2001: Populations*. Elsevier Applied Science, London and New York, pp. 831-850.
- Batzli, G.O., White, R.G., MacLean S.F. Jr., Pitelka, F.A. and Collier, B.D. 1980. The herbivore-based trophic system. In Brown, J., Miller, P.C., Tieszen, L.L. and Bunnell, F.L. (eds.), *An arctic ecosystem: the coastal tundra at Barrow, Alaska*. Dowden, Hutchinson, and Ross, Inc., Stroudsburg, Pennsylvania, pp. 335-410.
- Blackburn, G.S., Wilson, D.J., and Krebs, C.J. 1999. Dispersal of juvenile collared lemmings (*Dicrostonyx groenlandicus*) in a high-density population. *Can. J. Zool.*, in press.
- Boonstra, R. and Krebs, C.J. 1979. Viability of large- and small-sized adults in fluctuating vole populations. *Ecology* 60: 567-573.
- Bousfield, M.A. and Syroechkovskiy, Ye. V. 1985. A review of Soviet research on the Lesser Snow Goose on Wrangel Island, U.S.S.R. *Wildfowl* 36: 13-20.

- Boyd, H. 1989. Geese on Rowley Island, N.W.T., in 1987 and 1988. Canadian Wildlife Service Prog. Notes No. 181.
- Bromley, R.G., Heard, D. and Croft, B. 1995. Visibility bias in aerial surveys relating to nest success of arctic geese. *J. Wildl. Manage.* 59: 364-371.
- Brooks, R.J. 1993. Dynamics of home range in collared lemmings. In: Stenseth, N.C. and Ims, R.A. (eds.), *The Biology of Lemmings*. Academic Press, London, pp. 355-386.
- Brooks, R.J. and Banks, E.M. 1971. Radio-tracking study of lemming home range. *Comm. Behav. Biol.* 6: 1-5.
- Brown, J.H. and Lasiewski, R.C. 1972. Metabolism of weasels: the cost of being long and thin. *Ecology* 53: 939-943.
- Browne, R.H. 1979. On visual assessment of the significance of a mean difference. *Biometrics* 35: 657-665.
- Charnov, E.L. 1976. Optimal foraging; the marginal-value theorem. *Theor. Popul. Biol.* 9: 129-136.
- Chernyavski, F.B. 1979. Population dynamics and population indices of *Lemmus sibiricus* and *Dicrostonyx torquatus* on the Wrangel Island. *Zoologicheskii Zhurnal* 58: 553-563. [in Russian with English summary].
- Chernyavski, F.B. and Kiriushchenko, T.V. 1979. Reproduction and mortality of collared lemmings *Dicrostonyx torquatus* Pall. on Wrangel Island. In: *Ecology of voles and shrews in north-eastern Siberia*. Academy of Science of the U.S.S.R., Vladivostok. pp. 3-24. [In Russian.]
- Chernyavski, F.B., Kiriushchenko, S.P., and Kiriushchenko, T.V. 1981. Material concerning the winter ecology of Siberian lemming (*Lemmus sibiricus*) and collared lemming (*Dicrostonyx torquatus*): In: *Ecology of birds and mammals from Wrangel Island*. Nauka, Vladivostok, pp. 99-122. [In Russian.]
- Chitty, D. 1938. A laboratory study of pellet formation in the short-eared owl (*Asio flammeus*). *Proc. Zool. Soc. Lond. A* 108: 267-287.
- Chitty, D. 1952. Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire, in 1936-1939. *Philos. Trans. R. Soc. Lond. (B)* 236: 505-552.
- Chitty, D. 1960. Population processes in the vole and their relevance to general theory. *Can. J. Zool.* 38: 99-113.
- Chitty, D. 1996. *Do lemmings commit suicide? Beautiful hypotheses and ugly facts*. Oxford University Press, Oxford and New York.
- Chitty, H. and Chitty, D. 1962. Body weight in relation to population phase in *Microtus agrestis*. *Symposium Theriologicum, Brno, Czechoslovakia*, pp. 77-86.

- Christian, J.J. and Davis, D.E. 1966. Adrenal glands in female voles (*Microtus pennsylvanicus*) as related to reproduction and population size. *J. Mammal.* 47:1-18.
- Conover, W.J. 1980. Practical nonparametric statistics. Second edition. Wiley, New York.
- Cooke, F., Rockwell, R.F., and Lank, D.B. 1995. The snow geese of La Pérouse Bay. Oxford University Press, New York.
- Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51: 429-438.
- Cotter, R.C. 1991. Population attributes and reproductive biology of rock ptarmigan (*Lagopus mutus*) in the central Canadian arctic. M.Sc. Thesis, Univ. of Alberta, Edmonton.
- Craighead, J.J. and Craighead, F.C. Jr. 1969. Hawks, owls, and wildlife. Dover Publications, New York. (first published in 1956 by Stackpole Co. and the Wildlife Management Institute).
- Day, M.G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. *J. Zool.* 148: 201-217.
- Decisioneering. 1996. Crystal Ball version 4.0 user manual. Decisioneering, Denver CO.
- Desicoteaux, J.-P. and Mihok, S. 1986. Serologic study on the prevalence of murine viruses in a population of wild meadow voles. *J. Wildl. Diseases* 22:314-319.
- Desy, E.A. and Batzli, G.O. 1989. Effects of food availability and predation on prairie vole demography: a field experiment. *Ecology* 70: 411-421.
- Dhondt, A.A. 1987. Cycles of lemmings and brent geese *Branta b. bernicla*: a comment on the hypothesis of Roselaar and Summers. *Bird Study* 34: 151-154.
- Dorogov, V.F. 1983. Nesting of the rough-legged buzzard (*Buteo lagopus*) on Taimyr. In: Ecology and rational use of land vertebrates of North Central Siberia. *Sbornik Nauchnykh Trudov Sibirsk Otdel. VASKhNIL, Novosibirsk*, pp. 109-126. [in Russian].
- Dorogoy, I.V. 1983. Predators as a factor affecting lemming population dynamics in the tundra zone of north-eastern Siberia. Unpublished thesis. Biology and Soil Institute of the Far Eastern Scientific Centre, Academy of Science of the Soviet Union, Vladivostok. [In Russian.]
- Eberhardt, L.E., Hanson, W.C., Bengtson, J.L., Garrott, R.A., and Hanson, E.E. 1982. Arctic fox home range characteristics in an oil-development area. *J. Wildl. Manage.* 46: 183-190.
- Efron, B. and Tibshirani, R.J. 1993. An introduction to the bootstrap. Chapman and Hall, New York.
- Elton, C.S. 1924. Fluctuations in the numbers of animals: their causes and effects. *Br. J. Exp. Biol.* 2:119-163.

- Elton, C.S. 1942. Voles, mice and lemmings: problems in population dynamics. Clarendon Press, Oxford.
- Erlinge, S. 1987. Predation and noncyclicality in a microtine population in southern Sweden. *Oikos* 50: 347-352.
- Errington, P.L. 1946. Predation and vertebrate populations. *Quart. Rev. Biol.* 21: 144-177, 221-245.
- Fagerstone, K.A. 1987. Black-footed ferret, long-tailed weasel, short-tailed weasel, and least weasel. In: Novak, M., Baker, J.A., Obbard, M.E. and Malloch, B. (eds.), *Wild furbearer management and conservation in Ontario*. Ontario Ministry of Natural Resources, Toronto. pp. 549-573.
- Fitzgerald, B.M. 1977. Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. *J. Anim. Ecol.* 46: 367-397.
- Ford, R.G. and Pitelka, F.A. 1984. Resource limitation in populations of the California vole. *Ecology* 65:122-136.
- Frafjord, K. 1993. Energy intake of captive adult-sized arctic foxes *Alopex lagopus* in Svalbard, in relation to body weight, climate, and activity. *Z. Säugetierkunde* 58: 266-274.
- Frafjord, K. and Prestrud, P. 1992. Home range and movements of Arctic foxes *Alopex lagopus* in Svalbard. *Polar Biol.* 12: 519-526.
- Framstad, E., Stenseth, N.C. and Ostbye, E. 1993a. Time series analysis of population fluctuations of *Lemmus lemmus*. In: Stenseth, N.C. and Ims, R.A. (eds.), *The Biology of Lemmings*. Academic Press, London, pp. 97-116.
- Framstad, E., Stenseth, N.C. and Ostbye, E. 1993b. Demography of *Lemmus lemmus* through five population cycles. Pages 117-134 in Stenseth, N.C. and Ims, R.A. (eds.), *The Biology of Lemmings*. Academic Press, London, pp.117-134.
- Fuller, W.A., Martell, A.M., Smith, R.F.C. and Speller, S.W. 1975a. High arctic lemmings (*Dicrostonyx groenlandicus*). I. Natural history observations. *Can. Field-Nat.* 89: 223-233.
- Fuller, W.A., Martell, A.M., Smith, R.F.C. and Speller, S.W. 1975b. High arctic lemmings (*Dicrostonyx groenlandicus*). II. Demography. *Can. J. Zool.* 53: 867-878.
- Fuller, W.A., Martell, A.M., Smith, R.F.C. and Speller, S.W. 1977. Biology and secondary production of *Dicrostonyx groenlandicus* on Truelove Lowland. In: Bliss, L.C. (ed.). *Truelove Lowland, Devon Island: a high arctic ecosystem*. University of Alberta Press, Edmonton, pp. 437-459.
- Garrott, R.A. and Eberhardt, L.E. 1987. Arctic fox. In: Novak, M., Baker, J.A., Obbard, M.E. and Malloch, B. (eds.), *Wild furbearer management and conservation in Ontario*. Ontario Ministry of Natural Resources, Toronto, pp. 395-406.

- Gessaman, J.A. 1972. Bioenergetics of the snowy owl (*Nyctea scandiaca*). *Arct. Alp. Res.* 4: 223-238.
- Goszczyński, J. 1974. Studies on the food of foxes. *Acta Theriologica* 19: 1-18.
- Hanski, I., Turchin, P., Korpimäki, E., and Henttonen, H. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature* 364: 232-235.
- Hansson, L. 1984. Winter reproduction of small mammals in relation to food conditions and population dynamics. In: Merritt, J.F. (ed.), *Winter ecology of small mammals*. Special publication of the Carnegie Museum of Natural History, No. 10, Pittsburgh, PA. pp. 225-234.
- Henttonen, H. and Järvinen, A. 1981. Lemmings in 1978 at Kilpisjärvi: population characteristics of a small peak. *Mem. Soc. Fauna Flora Fennica*. 57: 25-30.
- Henttonen, H., Oksanen, T., Jortikka, A., and Haukisalme, V. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian tundra? *Oikos* 50: 353-365.
- Hersteinsson, P. and Macdonald, D.W. 1982. Some comparisons between red and arctic foxes, *Vulpes vulpes* and *Alopex lagopus*, as revealed by radio tracking. *Symp. Zool. Soc. Lond.* 49: 259-289.
- Hersteinsson, P. and Macdonald, D.W. 1996. Diet of arctic foxes (*Alopex lagopus*) in Iceland. *J. Zool. Lond.* 240: 457-474.
- Heske, E.J. and Jensen, P.M. 1993. Social structure in *Lemmus lemmus* during the breeding season. In: Stenseth, N.C. and Ims, R.A. (eds.), *The Biology of Lemmings*. Academic Press, London, pp. 387-409.
- Heske, E.J., Ims, R.A. and H. Steen. 1993. Four experiments on a Norwegian subalpine microtine rodent assemblage during a summer decline. In: Stenseth, N.C. and Ims, R.A. (eds.), *The Biology of Lemmings*. Academic Press, London, pp. 411-424.
- Hilborn, R. and Stearns, S.C. 1982. On inference in ecology and evolutionary biology: the problem of multiple causes. *Acta Biotheoret.* 31:145-164.
- Holling, C.S. 1959a. The components of predation as revealed by a study of small-mammal predation on the European pine sawfly. *Can. Entomol.* 91: 293-320.
- Holling, C.S. 1959b. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91:385-398.
- Holling, C.S. 1961. Principles of insect predation. *Ann. Rev. Entomol.* 6: 163-182.
- Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Pop. Biol.* 12: 197-229.

- Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.* 124: 377-406.
- Holt, R.D. and Lawton, J.H. 1994. The ecological consequences of shared natural enemies. *Ann. Rev. Ecol. Syst.* 25: 495-520.
- Jarrell, G.H. and Fredga, K. 1993. How many kinds of lemmings? A taxonomic overview. In: Stenseth, N.C. and Ims, R.A. (eds.), *The Biology of Lemmings*. Academic Press, London, pp. 45-57.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration stochastic model. *Biometrika* 52: 225-247.
- Kaikusalo, A. and Tast, J. 1984. Winter breeding of microtine rodents at Kilpisjärvi, Finnish Lapland. In: Merritt, J.F. (ed.), *Winter ecology of small mammals*. Special publication of the Carnegie Museum of Natural History, No. 10, Pittsburgh, PA. pp. 243-252.
- Kennedy, A.J. and Carbyn, L.N. 1981. Identification of wolf prey using hair and feather remains, with special reference to western Canadian National Parks. Canadian Wildlife Service, Edmonton, Alberta.
- Korpimäki, E. 1993. Regulation of multiannual vole cycles by density-dependent avian and mammalian predation? *Oikos* 66: 359-363.
- Korpimäki, E., Norrdahl, K. and Rinta-Jaskari, T. 1991. Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? *Oecologia* 88: 552-561.
- Korpimäki, E., Norrdahl, K., and Valkama, J. 1994. Reproductive investment under fluctuating predation risk: microtine rodents and small mustelids. *Evol. Ecol.* 8:357-368.
- Korpimäki, E. and Krebs, C.J. 1996. Predation and population cycles of small mammals. *BioScience* 46:754-764.
- Korpimäki, E. and Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. *Ecology* 79:2448:2455.
- Krebs, C.J. 1964a. The lemming cycle at Baker Lake, Northwest Territories, during 1959-1962. *Arct. Inst. N. Am. Tech. Pap.* 15.
- Krebs, C.J. 1964b. Cyclic variation in skull-body regressions of lemmings. *Can. J. Zool.* 42: 631-643.
- Krebs, C.J. 1978. A review of the Chitty hypothesis of population regulation. *Can. J. Zool.* 56:2464-2480.
- Krebs, C.J. 1989. *Ecological methodology*. HarperCollins, New York.

- Krebs, C.J. 1993. Are lemmings large *Microtus* or small reindeer? A review of lemming cycles after 25 years and recommendations for future work. In: Stenseth, N.C. and Ims, R.A. (eds.), *The Biology of Lemmings*. Academic Press, London, pp. 247-260.
- Krebs, C.J. 1995. Two paradigms of population regulation. *Wildl. Res.* 22:2-10.
- Krebs, C.J. 1996. Population cycles revisited. *J. Mammal.* 77: 8-24.
- Krebs, C.J., Keller, B.L. and Tamarin, R.H. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. *Ecology*, 50: 587-607.
- Krebs, C.J. and Myers, J.H. 1974. Population cycles in small mammals. *Adv. Ecol. Res.* 8: 267-399.
- Krebs, C.J., Boonstra, R. and Kenney, A.J. 1995. Population dynamics of the collared lemming and the tundra vole at Pearce Point, Northwest Territories, Canada. *Oecologia* 103: 481-489.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, Oxford.
- Lambin, X. 1993. Determinants of the synchrony of reproduction in Townsend's voles, *Microtus townsendii*. *Oikos* 67:107-113.
- Lee, E.T. 1980. *Statistical methods for survival data analysis*. Lifetime Learning Publications, Belmont, Ca.
- Lidicker, W.Z. and R.S. Ostfeld. 1991. Extra-large body size in California voles: causes and fitness consequences. *Oikos* 61: 108-121.
- Lima, S.L. and Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68: 619-640.
- Lockie, J.D. 1959. The estimation of the food of foxes. *J. Wildl. Manage.* 23: 224-227.
- MacLean, S.F., Jr., Fitzgerald, B.M. and Pitelka, F.A. 1974. Population cycles in arctic lemmings: winter reproduction and predation by weasels. *Arct. Alp. Res.* 6: 1-12.
- Maher, W.J. 1967. Predation by weasels on a winter population of lemmings, Banks Island, Northwest Territories. *Can. Field-Nat.* 81: 248-250.
- Maher, W.J. 1970. The pomarine jaeger as a brown lemming predator in northern Alaska. *Wilson Bull.* 82: 130-157.
- Maher, W.J. 1974. Ecology of pomarine, parasitic, and long-tailed jaegers in northern Alaska. *Pacific Coast Avifauna* 37: 148 pp.
- Malcolm, J.R. and R.J. Brooks. 1993. Cyclic variation in skull-body regressions of collared lemmings: differential representation of seasonal cohorts. In: Stenseth, N.C. and Ims, R.A. (eds.), *The Biology of Lemmings*. Academic Press, London, pp. 411-424.

- Mallory, F.F., Elliott, J.R., and Brooks, R.J. 1981. Changes in body size in fluctuating populations of the collared lemming: age and photoperiod influences. *Can. J. Zool.* 59: 174-182.
- Mangel, M. and Clark, C.W. 1988. *Dynamic modelling in behavioural ecology*. Academic Press, Princeton.
- Marcström, V., Kenward, R.E., and E. Engren. 1988. The impact of predation on boreal tetraonids during vole cycles: an experimental study. *J. Anim. Ecol.* 57: 859-872.
- Murdoch, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39:335-354.
- Murdoch, W.W. 1973. The functional response of predators. *J. Appl. Ecol.* 10:335:342.
- Norrdahl, K. and Korpimäki, E. 1995a. Mortality factors in a cyclic vole population. *Proc. Roy. Soc. Lond. B*:261:49-53.
- Norrdahl, K. and Korpimäki, E. 1995b. Effects of predator removal on vertebrate prey populations: birds of prey and small mammals. *Oecologia* 103: 241-248.
- Noy-Meir, I. 1981. Theoretical dynamics of competitors under predation. *Oecologia* 50: 277-284.
- Oksanen, T., Oksanen, L., and Fretwell, S.D. 1985. Surplus killing in the hunting strategy of small predators. *Am. Nat.* 126: 328-346.
- Otis, D. L., Burnham, K.P., White, G.C. and Anderson, D.R. 1978. *Statistical inference from capture data on closed animal populations*. Wildlife Monograph 62. 135pp.
- Pearson, O.P. 1971. Additional measurements of the impact of predation on California voles (*Microtus californicus*). *J. Mamm.* 52: 41-49.
- Pedersen, A. 1962. *Polar animals*. Taplinger, New York.
- Pitelka, F.A. 1973. Cyclic pattern in lemming populations near Barrow, Alaska. In: Britton, M.E. (ed.). *Alaskan Arctic Tundra: Proceedings of the 25th Anniversary Celebration of the Naval Arctic Research Laboratory*. Arct. Inst. N. Am. Tech. Pap. 25. pp. 199-215.
- Pitelka, F.A., Tomich, P.Q., and Treichel, G.W. 1955. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecol. Monogr.* 25: 85-117.
- Pollock, K.H. 1982. A capture-recapture design robust to unequal probabilities of capture. *J. Wildl. Manage.* 46: 757-760.
- Pollock, K.H., Winterstein, S.R., Bunck, C.M. and Curtis, P.D. 1989. Survival analysis in telemetry studies: the staggered entry design. *J. Wildl. Manage.* 53: 7-15.

- Pollock, K. H., Nichols, J.D., Brownie, C. and Hines, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107. 97 pp.
- Poole, K. G. and Boag, D.A. 1988. Ecology of gyrfalcons, *Falco rusticolus*, in the central Canadian Arctic: diet and feeding behaviour. *Can. J. Zool.* 66: 334-344.
- Prestrud, P. 1992. Denning and home-range characteristics of breeding arctic foxes in Svalbard. *Can. J. Zool.* 70: 1276-1283.
- Reid, D.G. 1995. Factors limiting population growth of non-cyclic collared lemmings at low densities. Ph.D. Thesis, Univ. of British Columbia, Vancouver.
- Reid, D.G., Krebs, C.J., and Kenney, A. 1995. Limitation of collared lemming population growth at low densities by predation mortality. *Oikos* 73: 387-398.
- Reid, D.G. and Krebs, C.J. 1996. Limitations to collared lemming population growth in winter. *Can. J. Zool.* 74: 1284-1291.
- Reid, D.G., Krebs, C.J., and Kenney, A.J. 1997. Patterns of predation on non-cyclic lemmings. *Ecol. Monogr.* 67: 89-108.
- Reynolds, J.C. and Aebischer, N.J. 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. *Mammal Rev.* 21: 97-122.
- Rodgers, A.R. and Lewis, M.C. 1986a. Diet selection in arctic lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*): forage availability and natural diets. *Can. J. Zool.* 64: 1684-1689.
- Rodgers, A.R. and Lewis, M.C. 1986b. Diet selection in arctic lemmings: demography, home range, and habitat use. *Can. J. Zool.* 64: 2717-2727.
- Roselaar, C.S. 1979. Fluctuaties in aantallen Krombekstrandlopers *Calidris ferruginea*. *Watervogels* 4: 202-210. [in Dutch with English summary].
- Sall, J. and Lehman, A. 1996. *JMP start statistics: a guide to statistics and data analysis using JMP and JMP IN software*. Duxbury Press at Wadsworth Publishing, Belmont CA.
- Scott, P.A. 1993. Relationship between the onset of winter and collared lemming abundance at Churchill, Manitoba, Canada: 1932-1990. *Arctic* 46: 293-296.
- Seber, G. A. F. 1965. A note on the multiple recapture census. *Biometrika* 52: 249-259.
- Semb-Johansson, A., Wiger, R., and Engh, C.E. 1979. Dynamics of freely-growing, confined populations of the Norwegian lemming *Lemmus lemmus*. *Oikos* 33:246-260.
- Seton, E.T. 1929. The arctic fox. In: *Lives of game animals*. Vol. 1. Doubleday, Doran, & Co. Garden City, NY. pp. 432-465.

- Shelford, V.E. 1943. The abundance of the collared lemming (*Dicrostonyx groenlandicus* (Tr.) var. *richardsoni* Mer.) in the Churchill area, 1929 to 1940. *Ecology* 24: 472-484.
- Simms, D.A. 1979. Studies of an ermine population in southern Ontario. *Can. J. Zool.* 57: 824-832.
- Sinclair, A.R.E. 1989. Population regulation in mammals. In: Cherrett, J.M. (ed.), *Ecological concepts*. Blackwell Scientific, Oxford, pp. 197-241.
- Sinclair, A.R.E., Olsen, P.D., and Redhead, T.D. 1992. Can predators regulate small mammal populations? Evidence from house mouse outbreaks in Australia. *Oikos* 59: 382-392.
- Sittler B. 1995. Response of stoats (*Mustela erminea*) to a fluctuating lemming (*Dicrostonyx groenlandicus*) population in North East Greenland: Preliminary results from a long-term study. *Annales Zoologici Fennici* 32: 79-92.
- Sklepkovych, B.O. and Montevecchi, W.A. 1996. Food availability and food hoarding behaviour by red and arctic foxes. *Arctic* 49: 228-234.
- Sokal, R.R. and Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. Third Edition. Freeman, New York
- Solomon, M.E. 1949. The natural control of animal populations. *J. Anim. Ecol.* 18: 1-35.
- Spaans, B., Blijleven, H.J., Popov, I.U., Rykhlikova, M.E., Ebbinge, B.S. 1998. Dark-bellied brent geese *Branta bernicla* forego breeding when arctic foxes *Alopex lagopus* are present during nest initiation. *Ardea* 86:11-20.
- Statistical Sciences. 1995. S-PLUS guide to statistical and mathematical analysis, Version 3.3. StatSci, a division of MathSoft, Inc., Seattle.
- Steen, H. 1995. Untangling the causes of disappearance from a local population of root voles (*Microtus oeconomus*): a test of the regional synchrony hypothesis. *Oikos* 73: 65-72.
- Steen, H., Holst, J.C. Solhøy, T. Bjerga, M. Klaussen, E. Prestegård, I. and Sundt, R.C. 1997. Mortality of lemmings (*Lemmus lemmus*) at peak density in a mountainous area of Norway. *J. Zool.* 243: 831-835.
- Stenseth, N.C. and Ims, R.A. 1993a. The history of lemming research: from the Nordic sagas to *The Biology of Lemmings*. In: Stenseth, N.C. and Ims, R.A. (eds.), *The Biology of Lemmings*. Academic Press, London, pp. 3-34.
- Stenseth, N.C. and Ims, R.A. 1993b. Population dynamics of lemmings: temporal and spatial variation - an introduction. In: Stenseth, N.C. and Ims, R.A. (eds.), *The Biology of Lemmings*. Academic Press, London, pp. 61-96.
- Stenseth, N.C., Bjørnstad, O.N., and Falck, W. 1996. Is spacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies. *Proc. Roy. Soc. Lond. B* 263:1423-1433.

- Stickney, A. 1991. Seasonal patterns of prey availability and the foraging behaviour of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. *Can. J. Zool.* 69: 2853-2859.
- Summers, R.W. 1986. Breeding production of dark-bellied brent geese *Branta bernicla bernicla* in relation to lemming cycles. *Bird Study* 33: 105-108.
- Summers, R.W. and Underhill, L.G. 1987. Factors related to breeding production of brent geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. *Bird Study* 34: 161-171.
- Syroechkovskiy, Ye.V., Litvin, K.Ye., and Ebbinge, B.S. 1991. Breeding success of geese and swans on Vaygach Island (USSR) during 1986-1988; interplay of weather and arctic fox predation. *Ardea*: 373-382.
- Taitt, M.J. and Krebs, C.J. 1985. Population dynamics and cycles. In: Tamarin, R.H. (ed.), *Biology of New World Microtus*. American Society of Mammalogists, pp.567-620.
- Tamarin, R.H., Reich, L.M., and Moyer, C.A. 1984. Meadow vole cycles within fences. *Can. J. Zool.* 62: 1796-1804.
- Tremblay, J.P., Gauthier, G., Lepage, D. and Desrochers, A. 1997. Factors affecting nesting success in greater snow geese: effects of habitat and association with snowy owls. *Wilson Bull.* 109: 449-461.
- Underhill, R.P., Prys-Jones, R.P., Syroechkovski, E.E. Jr., Groen, N.M., Karpov, V., Lappo, H.G., van Roomen, M.W.J., Rybkin, A., Schekkerman, H., Spiekman, H. and Summers, R.W. 1993. Breeding of waders (Charadrii) and brent geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis* 135: 277-292.
- Venables, W.N. and Ripley, B.D. 1997. *Modern applied statistics with S-Plus*. Second Edition. Springer, New York.
- White, G.C. 1998. Program MARK [Online]. Available: <http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>. [28 June 1998].
- White, G.C. and Bennetts, R.E. 1996. Analysis of frequency count data using the negative binomial distribution. *Ecology* 77: 2549:2557.
- Wolff, J.O. 1992. Parents suppress reproduction and stimulate dispersal in opposite-sex juvenile white-footed mice. *Nature* 359:409-410.