

PATTERNS OF PREDATION ON NONCYCLIC LEMMINGS

DONALD G. REID,¹ CHARLES J. KREBS, AND ALICE J. KENNEY

Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada, V6T 1Z4

Abstract. Noncyclic populations of microtine rodents may be limited within a relatively constant range of densities by generalist predators with a prey base sufficiently diverse to sustain them when rodents are scarce (generalist predator hypothesis). Collared lemmings (*Dicrostonyx kilangmiutak*) at Pearce Point, Northwest Territories, Canada, are noncyclic and limited to fairly constant low densities in summer by predation, principally by red fox and Rough-legged Hawks. We tested four predictions of the generalist predator hypothesis as a possible explanation for relatively constant lemming densities: (1) predators do not show strong numerical responses to lemming density; (2) the proportion of lemming biomass in predator diets declines with declining lemming abundance, compensated for by increased consumption of alternative prey; (3) predators show a type-III functional response to lemming density; and (4) at low densities, predation on lemmings ceases.

The first prediction was not satisfied by the principal predators: at very low lemming densities, Rough-legged Hawks did not settle, and breeding success of red foxes and hawks was limited by lemming abundance. However, a number of generalist predators (Golden Eagle, grizzly bear, arctic ground squirrel, Peregrine Falcon, and Gyrfalcon) did not respond numerically to the lowest lemming densities. The second prediction was partly supported: all predators consumed lemmings at a lower rate as lemming densities declined. However, Rough-legged Hawks were not able to compensate fully for the declining consumption by increasing their use of alternative prey, and red foxes were able to do so in one of three years. Regarding the third prediction, foxes showed some evidence of a type-III functional response but hawks did not. As for the fourth prediction, most predators still consumed lemmings at very low densities; lemmings lacked a secure refuge.

The Pearce Point system differs from those where microtine dynamics are relatively constant and nonirruptive because of persistent predation by generalists. In terms of biomass, lemmings are the principal prey for their dominant predators. These predators (the semigeneralist red fox and the specialist Rough-legged Hawk) rely on lemmings to breed, but drive them to densities too low to sustain breeding by these same predators in the subsequent spring. In this regard, the system is similar to one driven by specialists. In some winters, however, populations recover because lemmings breed under the snow and most summer predators are absent. As a result, lemming densities in spring are often high enough for specialists and semigeneralists to initiate breeding. When winter breeding and survival fail to allow population growth, hawks and foxes may fail to breed and then leave the system. Even so, summer generalists still persist and continue to consume lemmings, curtailing potential irruptive growth. In this regard, the system is similar to one where prey are relatively constant because of generalists.

Community dynamics at Pearce Point can best be understood as a combination of three dominant processes. Summer predation by specialists and semigeneralists results in destabilizing declines. Winter breeding, coupled with good survival, can lead to destabilizing growth. However, this growth is curtailed in the following summer by either destabilizing specialist predation or the stabilizing influence of generalist predation.

When lemmings are scarce, the semigeneralist red fox and some generalist predators rely on arctic ground squirrels as their primary prey or their principal alternative prey. The ground squirrel appears to be the critical species maintaining this relatively diverse arctic tundra predator community and the relatively constant lemming densities.

Key words: *arctic ground squirrel; collared lemming; Dicrostonyx kilangmiutak; generalist predator; predator diets; prey refuge; red fox; Rough-legged Hawk; semigeneralist predator; specialist predator.*

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¹ Present address: Fish and Wildlife Division, Ministry of Environment, Lands and Parks, P.O. Box 5000, Smithers, British Columbia, Canada, V0J 2N0.

INTRODUCTION

Many microtine rodent populations do not exhibit multiannual cyclicity with high-amplitude density changes, but fluctuate through changes of lower amplitude, often with an annual pattern (Taitt and Krebs 1985). Andersson and Erlinge (1977) proposed that more constant prey densities might result from limitation of population growth by (1) generalist predators, operating in a community with a relatively diverse prey base (generalist predator hypothesis), or (2) nomadic avian or mammalian predators responding rapidly in local abundance and breeding success to growing rodent populations (nomadic predator hypothesis). Hanski et al. (1991) showed, with mathematical modelling, that increasing the number of generalist predators in a predator-prey model with multiannual fluctuations reduced the amplitude and period of fluctuations, eventually to a stable equilibrium point.

Rosenzweig and MacArthur (1963), in a theoretical investigation of exploitative predator-prey systems, concluded that stability depended on: (1) sufficient alternative food to sustain the generalist predators when preferred prey are scarce; (2) relatively inefficient prey capture by these generalist predators, principally because prey have a secure refuge; and (3) predator population growth limited by some factor other than food (e.g., territoriality).

Some microtine rodent species include both populations with relatively constant densities and populations with high amplitude, multiannual density fluctuations (irruptions) in different portions of their range (Hansson and Henttonen 1985). The specialist predator hypothesis proposes that an irruption occurs when a population escapes limitation by specialist predators, which have few or no alternative prey when rodents become scarce (Andersson and Erlinge 1977, Hanski et al. 1993). In some other ecological communities, rodent irruptions occur despite the presence of generalist predators with a fairly diverse prey base. The rodent decline may still be driven by specialists. Generalist predators and their alternative prey also decline, probably because the alternative prey only partially compensate for declining rodents (Angelstam et al. 1984, Lindström et al. 1987).

The generalist-specialist distinction is not always clear. A true generalist keeps prey numbers within a narrow range, rapidly compensating for declines in one prey by using other prey. A true specialist can never fully compensate for declines in its prey, so it drives prey to lower levels, ultimately too low to sustain itself. Between these extremes, some predators ("semigeneralists") may compensate for declining primary prey to varying degrees, depending on annual circumstances or the prey base diversity.

At Pearce Point, Northwest Territories, Canada (69°48' N, 122°40' W), on the western arctic mainland coast, collared lemmings (*Dicrostonyx kilangmiutak*)

and tundra voles (*Microtus oeconomus*) remained at low densities (mostly <1/ha) over six years, along with a fairly stable and diverse predator community (Krebs et al. 1995, Reid et al. 1995). Mortality attributed to predators, principally red fox (*Vulpes vulpes*) and Rough-legged Hawk (*Buteo lagopus*), was sufficient and necessary to explain summer population declines of adult microtines, but the fates of subadults remained unclear (Reid et al. 1995). The constancy in prey numbers might be explained by the generalist predator or nomadic predator hypotheses, or some other set of community dynamics.

In this paper, we use predictions of the generalist predator hypothesis as a template for discussing how community dynamics at Pearce Point fit with other well-studied systems. In particular, we investigate the following predictions of the generalist predator hypothesis: (1) predators do not show strong numerical responses to variations in lemming density; (2) the proportion of lemming biomass in predator diets declines with decreasing lemming abundance, and is compensated for by increased consumption of alternative prey; (3) predators show weak functional responses at low lemming densities and stronger functional responses at higher lemming densities (type-III response); and (4) at very low lemming densities, predators consume virtually no lemmings due to low capture efficiency. We also test a prediction of our previous demographic study, that the majority of subadult lemmings born in summer are killed by predators (Reid et al. 1995).

METHODS

Study area

We conducted research in a 40-km² area immediately inland from Pearce Point, Northwest Territories, on the north coast of the western Canadian mainland, in summers 1987–1992, with more intensive study of predator-prey dynamics in 1990, 1991, and 1992. Gently rolling, glacially scoured hills were frequently broken by dolomite and basalt cliffs. Collared lemmings used three upland habitats: *Dryas integrifolia* heath, *D. integrifolia*/*Carex rupestris* heath, and *D. integrifolia*/*Carex membranacea* hummock communities (Krebs et al. 1995). Tundra voles were restricted to ribbon-like wet *Carex aquatilis* meadows and wetter hummock communities along stream and lake shores (Bergman and Krebs 1993, Krebs et al. 1995). Brown lemmings (*Lemmus trimucronatus*), extremely rare, were found only in one *Eriophorum*/*Carex* tussock meadow. A fourth resident vertebrate herbivore, the arctic ground squirrel (*Spermophilus parryi*), was widespread through the drier upland communities where well-drained soils provided excellent burrow sites. Caribou (*Rangifer tarandus*) were frequently present in mid to late summer.

The numerous cliffs provided excellent nesting habitat for several avian predators: Rough-legged Hawk

(*Buteo lagopus*), Golden Eagle (*Aquila chrysaetos*), Peregrine Falcon (*Falco peregrinus*), Gyrfalcon (*Falco rusticolus*), Raven (*Corvus corax*), Thayer's Gull (*Larus thayeri*), and Glaucous Gull (*L. hyperboreus*). The following alternative prey species were regular non-colonial nesters or summer residents within a 10-km inland radius of Pearce Point: Tundra Swan (*Cygnus columbianus*), Canada Goose (*Branta canadensis*), Common Eider (*Somateria mollissima*), Semipalmated Plover (*Charadrius semipalmatus*), Golden Plover (*Pluvialis dominica*), Baird's Sandpiper (*Calidris bairdii*), Pectoral Sandpiper (*Calidris melanotos*), Horned Lark (*Eremophila alpestris*), American Pipit (*Anthus rubescens*), Lapland Longspur (*Calcarius lapponicus*), and Snow Bunting (*Plectrophenax nivalis*). The following species were numerous on migration: Snow Goose (*Chen caerulescens*), Northern Pintail (*Anas acuta*), Oldsquaw (*Clangula hyemalis*), Red-breasted Merganser (*Mergus serrator*), and Sanderling (*Calidris alba*).

Microtine populations

We estimated population densities of lemmings and voles using the Jolly-Seber open population model. Small rodents were caught in Longworth traps during weekly or biweekly trapping sessions, and were individually marked with ear tags. We estimated densities on three areas (grids), each 18–25 ha, and with a range of vegetation communities (Reid et al. 1995). Because juveniles of summer cohorts were caught infrequently, densities are of resident microtines only (i.e., adults and subadults caught at least twice on the same grid). For further details on procedures, see Krebs et al. (1995) and Reid et al. (1995).

In all three years, lemmings with body mass >35 g (adults) were fitted with a radio transmitter (Biotrack, model SS-1) mounted to a cable tie as neck collar (total mass ≈3 g). Voles with body mass >35 g (larger adults) received radiocollars only in 1990. We relocated radiocollared individuals every 2–3 d, allowing us to accurately estimate time of death. To ascertain cause of death, we used: the location of radio in predator scats or pellets, or at dens or nests; predator sign (excavations, tracks, scats, whitewash) at rodent burrows or at the site where the carcass or radio was located; and the extent and pattern of carcass consumption.

At each capture, we recorded individual mass and reproductive condition. We estimated date of parturition using changes in mass, degree of closure of the pubic symphysis, and teat size. Lactating female *Dicrostonyx* typically use one maternal burrow (Brooks 1993; D. G. Reid, C. J. Krebs, and A. J. Kenney, unpublished data), and juveniles are weaned at 15–20 d (Brooks and Banks 1973). We assumed that a litter was not successfully weaned if, prior to the expected weaning date, either lactation ended or the female was found at least twice in a burrow >30 m from the natal burrow. These criteria are supported by data in Brooks (1993).

A small sample of litters born aboveground in traps, nest boxes, or sedge tussocks gave an estimate of mean litter size within 4 d of birth. By combining these data, we estimated the numbers of juveniles weaned per unit area.

Habitats

We mapped vegetation communities, as classified by Krebs et al. (1995), to quantify the regional availability of collared lemming habitats. For study grids, mapping was done on foot. For a regional assessment, digital Landsat data were used in a supervised classification of habitats. We assessed the area of each habitat type available to lemmings in two zones, obviously differing in abundance of the habitats. A coastal zone (21.82 km²), in which exposed sand and rock were more common, included all grids. An inland zone (832.96 km²) had relatively even vegetative cover, with little sand or rock.

Predator numerical responses

Numerical responses of predators included both the numbers of adults establishing breeding territories in spring and the numbers of young successfully weaned or fledged in summer. We lacked data on predator numbers in winter. In late May and early June, we searched all cliffs within the 40-km² study area, including areas up to 6 km inland from Pearce Point harbor, for raptors establishing nests or showing territorial behavior. We recorded clutch size, hatching success, and fledging success during subsequent visits to all cliffs in mid-June, early July, and early to mid August.

There was one red fox natal den in the 40-km² intensive study area. We periodically observed the den from a distance and visited it regularly to collect scats. From these observations, frequent sightings of foxes elsewhere, and the unique coat coloration of adult and weaned foxes, we counted numbers of adults and juveniles. We captured one nonlactating female in a Novak leg snare in June 1991, and marked her with a colored ear tag.

Ravens and Thayer's and Glaucous Gulls nested on inaccessible sea cliffs, and we were unable to accurately count active nests and breeding success. We did not accurately estimate populations of arctic ground squirrels, another lemming predator (Boonstra et al. 1990), in all years. However, we obtained an index of squirrel abundance in early July of 1991 and 1992 by placing microscope slides covered in talcum powder (see Boonstra et al. 1992) in all burrow mouths in four areas separated by ≥2 km, and counting the proportion of slides tracked by squirrels within 24 h. Also in 1992, we combined live trapping (Tomahawk traps) and colored ear-tagging of squirrels at all burrows on three 1-km² study blocks, with periodic observations of the blocks, to get an absolute count of adult squirrels prior to weaning of juveniles. Ermine (*Mustela erminea*) were summer and winter residents, and bred in the

study area each summer, judging by casual observations, but we did not make a precise population estimate. We estimated grizzly bear (*Ursus arctos*) numbers from occasional sightings and track sizes.

Predator diets

Collections.—We collected pellets of all resident raptorial birds, except the raven, and scats of two mammalian predators, the red fox and grizzly bear. Regurgitated pellets of raptors and gulls were collected systematically at egg-laying in late May and early June (pre-incubation sample), at hatching in late June and early July (incubation sample), and at fledging in mid to late August (nestling sample) (cf. Poole and Bromley 1988), at a series of obvious raptor perches (cliff tops, glacial erratics, rock outcrops) throughout the study area. The 1990 collections did not include perches used by gulls or Golden Eagles; the collection area was expanded in 1991 and 1992 to sample these species. Because eagle eggs hatch in early June at this latitude (Poole and Bromley 1988), all eagle pellets were lumped together as a nestling collection. Nearly all gull pellets were probably from Glaucous Gulls, judging by observations of perch use by gulls. To minimize disturbance, we did not collect pellets and prey remains at or below nests during the reproductive period. At each collection, every pellet was removed, its length and maximum diameter were recorded, and it was individually bagged and labelled.

We collected fox scats systematically from the same sites as the raptor pellets, systematically from the natal den and two other intermittently used dens, and opportunistically whenever fresh scats were found. Systematic collections were monthly in 1990, and bi-weekly in 1991 and 1992. At each collection, every scat was removed, its maximum diameter was recorded, and it was individually bagged and labelled. Most scats were collected at the natal den. This sample probably consisted of scats from adults and juveniles, which might have had different diets. We used the frequency distribution of maximum diameters of scats to differentiate juvenile from adult scats.

We collected all grizzly bear scats encountered.

Analyses.—Fox scats were autoclaved and soaked in water for 24–72 h to loosen material. To remove soluble material, we washed scats through a series of sieves, with a paper towel on top of the lowest sieve to catch small, undigested remains. Remains were air-dried. All bones (as small as microtine molar teeth), large feathers, eggshell, insect parts, and large pieces of vegetation were separated by hand, leaving a set of remains consisting mostly of mammalian hair, sometimes mixed with small pieces of feathers, vegetation, and inorganic debris (mostly sand). The percentage by mass of each component of this latter set of remains was estimated by eye, taking account of the higher density of inorganic debris. All were weighed (± 0.05 g).

We identified remains to species (mammals), or order

(birds, insects), using reference material from the field and from museum collections, and using molar teeth descriptions in Banfield (1974), hair keys in Kennedy and Carbyn (1981) and Adorjan and Kolenosky (1969), and feather keys in Day (1966).

Since molar teeth are the most recognizable microtine remains in fox scats (Lockie 1959), and each of the 12 molar teeth of each of the three microtines in our study area is unique, we recorded the frequency of each molar tooth in each scat. When remains included two microtines, we calculated the relative proportions of hair and bone mass based on the relative proportions of molar teeth (Lockie 1959). When microtine skeletal material was lacking, we differentiated voles from lemmings by hair color.

Raptor pellets and bear scats were separated by hand into the same sets of remains as fox scats, and components were identified using the same reference material and keys.

Conversions to biomass.—For fox scats, we used information in Lockie (1959), Goszczynski (1974), and Reynolds and Aebischer (1991) to provide the following multiplicative factors to convert total mass of undigested remains by species (mammals) or order (birds) to biomass of prey eaten: voles (23), ground squirrels (45), large mammals such as caribou and grizzly bear (100), passeriform and charadriiform (“small”) birds (45), anseriform and galliform (“large”) birds (61), and eggshell (9.1). For lemmings, we used a factor of 28, because adult lemmings are substantially larger, with shorter appendages and a more globular body form with lower surface-to-volume ratio, compared to the vole species studied by Lockie (1959) and Goszczynski (1974). Insects were ignored in biomass estimations, since they were mostly in trace quantities. We assumed that foxes ate a similar proportion of ground squirrel carcasses as they would lagomorphs. The factor of 100 for large mammals is intermediate to factors provided by Lockie (1959) and Goszczynski (1974).

An alternative approach to biomass estimation, suggested for foxes by P.-O. Palm (*unpublished data*) and for ermine by Gamberg and Atkinson (1988), assumes that mammalian hair is not digested at all. This is a valid assumption, judging by the microscopic appearance of hair in fox scats. To determine the relationship between hair and body mass, we removed hair from pelts of 14 *Dicrostonyx*, collected by Dr. N. Larter on Banks Island, Northwest Territories, by soaking pelts in water for a few days and gradually scraping away the hair (Gamberg and Atkinson 1988). A conversion factor was derived from the mass of hair as a proportion of body mass.

For raptors, conversion factors relating remains in pellets to biomass ingested were unavailable. Mandible length is a good predictor of body mass (Hamilton 1980), but mandibles were partially digested in most pellets. However, the molar tooth rows on dentary and maxillary bones were frequently intact, along with nu-

merous separate molar teeth. We used these to assess lemming biomass ingested, assuming that: (1) all lemming heads are ingested, (2) all lemmings ingested are represented by at least one tooth, and (3) lengths of the molar tooth rows are significant predictors of body mass. To test the first two assumptions for Rough-legged Hawks, volunteers fed freshly thawed lemmings, originally from a laboratory colony, to a captive hawk in a $5 \times 5 \times 3$ m outdoor aviary (Orphaned Wildlife Rehabilitation Centre, OWL, Delta, British Columbia), at approximately midday in April, and at two rates: two lemmings per day for 7 d, followed by four lemmings per day for 13 d. Pellets were collected daily, and the hawk was weighed at the beginning and end of each period. Light regimes differed from the 24-h daylight of an arctic summer, but temperature regimes were not much warmer at the southern latitude of the experiment. To test the third assumption, we measured tooth row lengths of 17 collared lemmings collected on Banks Island, N.W.T., in summer 1993.

Conversion to number of individuals killed.—For foxes, we estimated daily consumption rates (grams per day) in each time period from lemming biomass (grams) per scat by multiplying by an assumed defecation rate (scats per day). This consumption rate (grams per day) was converted to numbers of individual adult and subadult lemmings consumed each day, based on the proportions of adults and subadults in the diet for that time period and the mean live mass (grams) of these age classes in the population, based on live trapping during the same time period.

For foxes, daily defecation rate varies from 1–6 scats for a poorly fed fox (ingesting 200 g/d) to 8–12 scats for a well-fed fox (600–800 g/d), giving a reasonable mean 7 scats/d for an intermediate diet of 300–500 g/d (P.-O. Palm, unpublished data).

To differentiate adult (>35 g) from subadult (<35 g) lemmings in scats, we used the bony parts most frequently found intact (ulna and upper and lower molar tooth rows), and for which a linear dimension varied with body size. We used a sample of 17 collared lemmings from Banks Island to determine the regression relationships between body mass and the lengths of these bony parts. For each collection period, we assumed that the ratio of subadults to adults in scats represented the relative proportions of those age classes ingested. We also assumed that subadult remains represented only weaned individuals, since bones of suckling juveniles are brittle and unlikely to pass intact through fox digestive tracts.

For Rough-legged Hawks, we used the captive-feeding experiment to determine what proportion of lemmings ingested was represented by unique molar teeth in pellets, and then to calculate a conversion factor relating the number of individuals in pellets (maximum number of unique molar teeth) to the number of individuals ingested. We used this experiment to test the assumption that the ratio of adult to subadult lemmings

in pellets, as determined by molar tooth row lengths, represented the relative proportions of these age classes ingested. Calculating daily consumption rates depends on the casting rate of pellets, which we calculated from this feeding experiment.

For foxes and hawks, we estimated the sex ratio of lemmings ingested from the incidence of undigested male and female pelvic bones, differentiated by ischium length and pubis width (Dunmire 1955).

Total impact of predation.—We converted daily rates at which foxes consume adult and subadult lemmings to total impact for the time period, multiplying by the number of foxes (adult or juvenile) present during the time period and by the length of the period (days). We summed the results from each time period to give total impact over the summer.

We estimated the area used by foxes in summer to kill all the adult lemmings found in scats from the numbers of adult radio-collared lemmings killed on study grids over a summer, and from the area of collared lemming habitat on study grids and in the two regional zones of differing habitat availability. Collared lemmings were located 97% of the time in three habitat types (*Dryas* heath, *Dryas/Carex* heath, and *Carex/Dryas* hummock; Krebs et al. 1995), considered collectively as lemming habitat. Lemming habitat made up 36.6 ha of the grids where mortality data were collected, allowing a calculation of numbers killed per hectare of lemming habitat. Foxes hunted throughout the coastal zone, so the number of lemmings they killed in this zone was the number killed per hectare of lemming habitat multiplied by the number of hectares of lemming habitat in this zone. The remainder of their kill was from the inland zone. We estimated the area of inland zone they used from counts of numbers killed per hectare of lemming habitat on study grids, and the proportion of lemming habitat in the inland zone. The total estimated area traversed by foxes was the entire coastal zone plus the area of the inland zone required for the remaining kill.

To calculate the impact of fox predation on subadult lemmings, we assumed that subadults were weaned in lemming habitat and killed within the area traversed by foxes hunting adults. We estimated numbers of subadults available from our data on mean litter size, number of litters weaned per hectare of lemming habitat on study grids, and the total area of lemming habitat in the area traversed by hunting foxes.

We calculated the total impact of adult Rough-legged Hawk predation in the same manner as for red fox predation. However, we lacked data on nestling diets.

Predator functional responses

For foxes and Rough-legged Hawks, daily rates at which adult lemmings were consumed were taken from the scat and pellet analyses and plotted against the adult lemming density for the same time period, estimated as the mean of densities on our three grids. We lacked

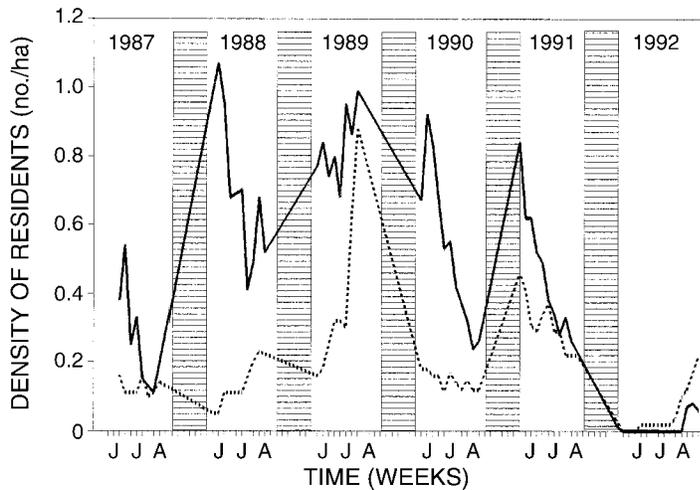


FIG. 1. Mean Jolly-Seber density estimates (no./ha) of resident collared lemmings (solid line) and tundra voles (broken line) on the three study grids in six summers of study. Striped bars represent winter, during which densities are interpolated.

solid data on subadult lemming density, so cannot include this age class in functional responses.

RESULTS

Microtine demography

Densities of resident *Dicrostonyx* declined sharply during most summers, sometimes recovering in winter (Fig. 1). Lemmings increased in 1989, when casual observations indicated that foxes were largely absent, and in 1992 when foxes emigrated (Table 1). *Microtus* densities were more constant in summer, sometimes increasing, and did not show strong growth in winters. Both species virtually disappeared in winter 1991–1992, remaining absent or at extremely low densities

through summer 1992 until late August (Fig. 1). The standard deviation of logarithmic transformations of densities (s) at the end of the summers was 0.40, which, combined with the persistent low densities, indicates that the lemmings were not cyclic (see Henttonen et al. 1985).

Red foxes and Rough-legged Hawks together caused between 57% (1991) and 72% (1990) of all confirmed predation mortalities of adult lemmings (Table 2). A number of the mortalities attributed to an unspecified raptor could have been Rough-legged Hawk, Peregrine Falcon, or gull kills. Ermine were rare on grids in summer but used them more in winter (Reid et al. 1995). Our general observations indicated that ermine stayed close to rocky cover in summer.

TABLE 1. Numbers of raptor pairs establishing breeding territories, numbers of successful nests and fledglings, and numbers of adult and weaned juvenile mammalian predators, in relation to adult *Dicrostonyx* density (no./ha, mean \pm 1 SE) and combined adult *Dicrostonyx* and *Microtus* densities (no./ha) in spring (early June) and summer (early July) on three study grids.

| Demographic variables | 1990 | 1991 | 1992 |
|--|-----------------|-----------------|-----------------|
| Spring densities | | | |
| <i>Dicrostonyx</i> | 1.03 \pm 0.34 | 0.84 \pm 0.24 | 0.01 \pm 0.01 |
| Both microtines | 1.15 \pm 0.43 | 1.09 \pm 0.13 | 0.03 \pm 0.03 |
| Summer densities | | | |
| <i>Dicrostonyx</i> | 0.73 \pm 0.28 | 0.62 \pm 0.16 | 0 \pm 0 |
| Both microtines | 0.88 \pm 0.34 | 0.88 \pm 0.31 | 0.01 \pm 0.01 |
| Raptor territorial pairs | | | |
| Rough-legged Hawk | 4 | 6 | 0 |
| Peregrine Falcon | 5 | 5 | 6 |
| Golden Eagle | 1 | 1 | 1 |
| Gyrfalcon | 0 | 0 | 1 |
| Successful nests (no. fledglings) | | | |
| Rough-legged Hawk | 2 (3) | 3 (5) | 0 |
| Peregrine Falcon | 5 (10) | 2 (2) | 4 (10) |
| Golden Eagle | 1 (1) | 1 (1) | 1 (2) |
| Gyrfalcon | 0 | 0 | 1 (2) |
| Mammal adults (no. weaned young) | | | |
| Red fox | 2 (3) | 3 (2) | 3 to 1 (0) |
| Ermine | ? (\geq 2) | ? (\geq 3) | ? (\geq 2) |
| Grizzly bear | 1 (0) | 1 (0) | 2 (0) |

TABLE 2. Numbers of confirmed predation mortalities of radio-collared adult collared lemmings attributable to individual predator species. The sex ratio (male : female) of adults killed by the two principal predators is indicated in parentheses.

| Predator species | 1990 | 1991 | 1992 |
|------------------------|-----------|-----------|------|
| Red fox | 21 (7:14) | 4 (2:2) | 0 |
| Suspected fox | 5 | 4 | 0 |
| Arctic ground squirrel | 0 | 2 | 0 |
| Grizzly bear | 0 | 2 | 0 |
| Ermine | 0 | 0 | 0 |
| Rough-legged Hawk | 7 (4:3) | 17 (11:6) | 0 |
| Peregrine Falcon | 0 | 1 | 1 |
| Unknown raptor | 6 | 7 | 0 |
| Total | 39 | 37 | 1 |

For lemmings, litter size across all cohorts and all years was 5.0 ± 0.27 (mean ± 1 SE, $n = 27$). Lemmings weaned 14 litters in 1990 on study grids exposed to predation (36.6-ha lemming habitat), and seven litters in 1991.

Numerical responses of predators

Microtine densities differed little between 1990 and 1991, but both species were extremely rare in 1992 (Table 1, Fig. 1). Red foxes and Rough-legged Hawks showed obvious numerical responses to low microtine densities in 1992 (Table 1). Three red foxes died during the 1991–1992 winter. The female ear-tagged in 1991 was seen at the den with one pup on 14 June 1992, but not again. The den was virtually unused after 21 June, and only one of three adults from June was seen later in the summer. At least two Rough-legged Hawk pairs were seen in late May 1992, but none nested. By contrast, three other raptor species and the other mammalian predators showed little or no numerical response to the very low microtine densities in 1992 (Table 1). Numbers of nesting gulls of both species were noticeably lower in 1992, perhaps in response to low lemming densities, but we lacked quantitative data.

Steep summer declines in lemming abundance in 1990 and 1991 appeared to affect red fox and Rough-legged Hawk breeding success. In 1991, only two of five fox known fox pups were weaned. In early July 1990, Rough-legged Hawks abandoned two nests (eight eggs) just prior to hatch, and three young fledged from the remaining two nests. In 1991, three pairs of hawks abandoned nests (11 eggs) in late June, close to hatch,

and five young fledged from three other nests. Chicks were food stressed, judging by aggression of larger chicks aimed at smaller ones, and discovery of chick remains below two nests.

In contrast, Peregrine Falcons fledged 10 young from 14 eggs in 1990, and also in 1992 when lemmings were scarce. Their low success in 1991 (two fledged from 16 eggs) resulted from predation on one nest and two intense storms, one of which washed a nest off a cliff and the other hitting when young were downy but quite large. In 1992, Gyrfalcons and Golden Eagles fledged all young hatched. At least one gyrfalcon used the area in 1990, but we found no evidence of nesting.

The proportion of microscope slides with ground squirrel tracks on four areas was 0.38 ± 0.12 (all values mean ± 1 SE) in 1991 and 0.17 ± 0.06 in 1992, indicating a decline between years. In 1992, 11 resident squirrels occupied 3 km² prior to the emergence of young. The density of double burrows (cf. Carl 1971) was 9.3 ± 1.4 burrows/km² (mean ± 1 SE, $n = 4$ 1-km² blocks).

Grizzly bears occasionally visited the study area, each one spending 2–10 d in a summer. One denned in the area in winter 1990–1991.

In 1990 and 1991, one pair of Rough-legged Hawks (RLH) nested 7 km west on the coast, and in all years a pair of Peregrine Falcons (PF) nested 7 km inland, but we lack complete data on these nests. Beyond these, the nearest raptor nests (RLH and PF) were 12.5 km inland, where one pair of RLH nested in 1992, suggesting that microtine densities inland may have been higher than on the coast.

In summary, for numerical responses, Rough-legged Hawks, red foxes, and perhaps Glaucous Gulls, acted as specialists, whereas grizzly bears, Golden Eagles, Peregrine Falcons, and Gyrfalcons acted as generalists.

Predicting lemming body mass

Ulna length, mandible length (cf. Hamilton 1980), upper and lower molar tooth row lengths, and hair mass were all significant predictors of live body mass for *Dicrostonyx* (Table 3). Hair comprised $2.8 \pm 0.14\%$ (mean ± 1 SE) of body mass, giving a conversion factor of mass of hair in scats to body mass ingested of 36.

Fox diet

Differentiating adult and juvenile scats.—Fox scats at the natal den increased in maximum diameter from

TABLE 3. Linear regressions of live body mass (g) of *Dicrostonyx* (dependent variable) on lengths (cm) of mandible, ulna, and upper and lower molar tooth rows, and from mass (g) of hair. The latter regression was forced through the origin, and r^2 is calculated accordingly.

| Independent variable | Regression equation | n | r^2 | F | df | P |
|----------------------|----------------------------------|-----|-------|-------|-------|--------|
| Mandible length | $\log y = 0.855 + 4.367 \log x$ | 16 | 0.73 | 37.1 | 1, 14 | <0.001 |
| Ulna length | $\log y = 1.012 + 2.684 \log x$ | 17 | 0.91 | 146.8 | 1, 15 | <0.001 |
| Upper tooth row | $\log y = -2.626 + 4.954 \log x$ | 17 | 0.85 | 84.6 | 1, 15 | <0.001 |
| Lower tooth row | $\log y = -1.783 + 4.011 \log x$ | 17 | 0.80 | 60.9 | 1, 15 | <0.001 |
| Hair mass | $y = 34.45 x$ | 14 | 0.74 | | | |

Snow Bunting at the natal den. Gallinaceous bird remains were probably Rock Ptarmigan (*Lagopus mutus*), which were very rarely seen in the study area but may have been more common inland. Most insect remains were bumble bees (*Bombus* sp.), and an unidentified crab species comprised the crustacean remains.

In June 1992, fox diet was similar to that in late summer 1990 and 1991 (Tables 4 and 5), with a relatively high incidence and biomass of birds and mammals other than lemmings. This pattern appeared to be directly related to the extremely low lemming densities. Foxes still managed to find lemmings, perhaps by travelling inland or by finding pockets of higher density than on grids.

For scats of adult foxes, estimates of lemming biomass derived from combined mass of bone and hair (conversion factor 28) were very similar to those derived from hair mass alone in 1990 and 1991, but conversion from hair mass gave slightly higher estimates in 1992, perhaps because of more complete digestion of bone by food-stressed foxes (Table 5). For juvenile scats, estimates derived from hair mass were consistently lower, possibly because of poorer digestive efficiency of juvenile foxes (Lockie 1959).

Juvenile diets were less diverse than adult diets (Tables 5 and 6). They completely lacked large mammals and virtually lacked eggs, but had higher proportions of lemmings. These patterns are reasonable because juveniles are provisioned by adults. However, adult foxes apparently consumed more ground squirrel and large bird prey than they provided to juveniles.

Daily consumption.—The numerical responses of foxes indicated some food stress in midsummer 1991 (pup mortality) and severe stress in 1992 (no pups weaned; disappearance of adults), so defecation rates were likely to be lower in these periods. Biomass per scat remained high in 1990 but declined in 1991, another indication of food stress. We assumed that there was no food stress in 1990 or June 1991 (defecation rate of 7 scats/d), and some stress in July and August 1991 (6 scats/d). In 1992, we assumed a rate of 4 scats/d (Table 7).

Total daily consumption was highest in early June, comprised mostly of lemmings at a time when lemmings were particularly vulnerable, with snow melting and flooding burrows (Table 7). Daily consumption of lemmings dropped strongly by July and tended to fall through the rest of the summer.

Total daily consumption did not decline strongly through summer 1990 (Table 7). Foxes compensated for declines in lemming consumption by increased consumption in July and August of voles, large birds, and particularly ground squirrels (Table 4). In 1991, however, foxes did not fully compensate for the June–August declines in lemming consumption until their consumption of ground squirrels increased substantially in late August (Table 4). Adult consumption fell well below 1990 levels by early August, and juvenile con-

sumption was less than in 1990. Foxes already fed quite heavily on voles and ground squirrels in June and July, and appeared unable to increase this feeding to make up for the decline in lemming consumption. In early June 1992, total daily consumption was remarkably high despite low lemming consumption. However, foxes were unable to sustain their use of alternative prey by mid-June and July, when consumption of all species declined.

Impact on the lemming population.—The three habitats used by lemmings made up 56.1% of the coastal zone and 90.9% of the inland zone. In 1990, foxes consumed ≈ 1430 adult lemmings (Table 7). Twenty-one adult lemmings (31% of the adult population) were killed by foxes on the 36.6 ha of lemming habitat on study grids (Table 2). This converts to 702 adults killed in the coastal zone (21.82 km²), with the remainder being killed in 12.68 km² of lemming habitat, or 13.94 km² total area, in the inland zone. In 1990, the fox population required a minimum area of 35.76 km².

In 1991, foxes killed a minimum of four adult lemmings (8% of all adults) on study grids. This converts to 134 adults in the coastal zone, the remainder (1105) being killed on 101.38 km² of lemming habitat, or 111.48 km² total area, inland. In 1991, the total area hunted by foxes was 133.30 km². Actual predation impacts and areas used by foxes are probably intermediate between these quite different annual estimates.

In 1990, the estimated fox hunting range included 2491 ha of lemming habitat. Lemmings weaned 0.38 litters/ha of habitat, with a mean litter size of five. This converts to 4733 weaned subadults. Of these, an estimated 2189 (46.2%) were killed by foxes (Table 7). In 1991, the hunting range included 11 361 ha of lemming habitat, and lemmings weaned 0.19 litters/ha of habitat, or 10 793 weanlings. Of these, 1852 (17.2%) were killed by foxes. The percentage killed in either year was probably intermediate between these estimates.

Foxes tended to take more female than male lemmings during summer, based on deaths of radio-collared adults (Table 2) and on the ratio of male to female pelvic bones in scats: 0:4 in 1990 and 12:14 in 1991.

Functional response.—The number of adult lemmings eaten per day per adult fox increased with adult lemming density ($y = 7.486x$; $r^2 = 0.87$; $F = 72.556$; $df = 1, 10$; $P < 0.001$; Fig. 3). Up to an adult lemming density of 0.65/ha, foxes modestly increased the number of adult lemmings killed each day. These data were from July and August, when the diet was comprised largely of prey other than lemmings. At lemming densities >0.65 /ha (mostly in June), foxes appeared to increase their kill rate more dramatically (Fig. 3). This contrast suggests the curvilinearity of a type-III response, and slightly more of the variance is explained by an exponential model ($y = 10.995x^2$; $r^2 = 0.91$). However, the 1992 data reflect the virtual absence of lemmings on study grids, which must have underestimated regional densities. The fit of the exponential

TABLE 5. Biomass (g, mean \pm 1 SE) per scat for adult red fox, and percentage of total biomass (in parentheses) of principal prey groups. All biomass estimations are based on conversion of all prey remains, except for *Dicrostonyx*^a, which is based on hair alone. *N* is the sample size of scats.

| Prey type | 1990 | | | 1991 | | |
|---------------------------------|-------------------------|------------------------|------------------------|-------------------------|------------------------|------------------------|
| | June | July | August | 2–22 June | 23 June–6 July | 7–20 July |
| <i>N</i> | 13 | 44 | 38 | 29 | 27 | 33 |
| <i>Dicrostonyx</i> ^a | 66.2 \pm 10.8 (78) | 35.3 \pm 5.1 (40) | 34.0 \pm 6.0 (42) | 80.2 \pm 13.0 (67) | 26.9 \pm 6.1 (36) | 35.7 \pm 6.9 (51) |
| <i>Dicrostonyx</i> ^b | 67.6 \pm 10.0 (80) | 36.2 \pm 5.4 (41) | 34.3 \pm 5.9 (42) | 80.0 \pm 12.0 (67) | 29.0 \pm 6.2 (39) | 35.0 \pm 5.9 (50) |
| <i>Microtus</i> | 3.2 \pm 3.2 (4) | 11.1 \pm 3.4 (12) | 2.8 \pm 1.3 (3) | 5.2 \pm 2.8 (4) | 6.6 \pm 2.7 (9) | 9.9 \pm 3.1 (14) |
| <i>Spermophilus</i> | 1.4 \pm 1.4 (2) | 9.8 \pm 4.0 (11) | 30.1 \pm 6.4 (37) | 17.7 \pm 7.1 (15) | 29.3 \pm 6.7 (39) | 13.2 \pm 3.6 (19) |
| Large mammal | 4.6 \pm 3.3 (5) | 3.8 \pm 1.8 (4) | 3.2 \pm 1.7 (4) | 1.7 \pm 1.4 (1) | 0.2 \pm 0.2 (0) | 0.9 \pm 0.9 (1) |
| Large bird | 7.0 \pm 6.0 (8) | 25.4 \pm 8.9 (29) | 10.2 \pm 3.5 (12) | 10.9 \pm 6.8 (9) | 5.4 \pm 4.4 (7) | 7.5 \pm 4.7 (11) |
| Small bird | <0.1 (0) | 2.7 \pm 2.2 (3) | 0.9 \pm 0.7 (1) | 3.3 \pm 2.5 (3) | 4.8 \pm 2.1 (6) | 3.2 \pm 0.9 (5) |
| Egg | 0.6 \pm 0.5 (1) | 0.1 \pm 0.1 (0) | 0.3 \pm 0.2 (0) | 0.1 \pm 0.1 (0) | <0.1 (0) | 0.5 \pm 0.2 (1) |
| Total | 84.8 \pm 11.5 | 89.1 \pm 9.3 | 81.8 \pm 6.9 | 118.9 \pm 15.0 | 75.1 \pm 6.2 | 70.2 \pm 9.2 |

model may be biased by these data. Perhaps the changes in fox diet represent switching from adult lemmings to other prey items, but subadult lemmings were a considerable portion of the “alternative” prey. Therefore, the functional response of foxes to the entire lemming population is unclear. Even when lemmings were rare (< 0.20/ha), foxes still continued to consume one or two each day. Thus, the lemmings lacked a low-density refuge.

In summary, foxes can be classed as semigeneralists with regard to diet. They fully or partially compensate for declining lemming abundance with alternative prey. They sharply increase their consumption of lemmings with increasing lemming density, perhaps in a type-III fashion.

Grizzly bear diet

Of 16 bear scats collected over three summers, 10 (63%) contained arctic ground squirrel remains and three (19%) contained collared lemming remains.

Rough-legged Hawk feeding experiment

When fed two lemmings per day, the captive hawk lost some body mass, digested lemmings more thoroughly, and cast pellets at a slightly lower rate than when fed four lemmings per day, when it gained body mass (Table 8). It discarded no lemming heads, and generally swallowed lemmings whole, up to four at a time. It removed the gastrointestinal tract more frequently when fed at the higher rate. It consumed all food offered within 24 h, except for one day at the higher rate, when two lemmings were ignored. Based on the proportion of lemmings fed that were recovered in pellets (Table 8), we derived the following correction factors to convert number of individual lemmings in

pellets to number ingested: 1.27 when slightly food stressed (74 g/d); and 1.02 when well-fed (137 g/d).

Over the entire experiment, the ratio of adult to subadult lemmings offered was 26:28, but the ratio recovered in pellets, based on intact molar tooth rows in dentary and maxillary bones, was 9:4. Of adults fed to the hawk, 34.6% were recovered with at least one tooth row intact, whereas only 14.3% of subadults were recovered. We use these proportions to correct observed ratios in pellets collected in the field.

Rough-legged Hawk diet

Composition.—In percentage frequency of occurrence, lemmings dominated the Rough-legged Hawk diet throughout the summer (Table 9). The amount of lemming biomass ingested dropped substantially in late summer (Table 10), and hawks consumed an increasing percentage of voles, ground squirrels, and birds (Table 9).

We lacked data to convert remains of each alternative prey to biomass ingested. However, if we assumed the same correction factors and casting rates for pellets with voles as for those with lemmings, and used mean vole mass from live trapping (both age classes combined), then the voles provided between 3.9 and 9.2 g/d. This does little to compensate for the declining rate of lemming consumption. Given the high rate of nest abandonment close to hatching, it appeared that many Rough-legged Hawk pairs were unable to compensate for the declining rate of lemming consumption. A few pairs each year were able to kill sufficient alternative prey to feed themselves and a few young. Prey remains after two young fledged from one nest in 1990 included one ground squirrel, two *Calidris* sandpipers, one duck, and small passerine feathers.

TABLE 5. Continued.

| 1991 | | | 1992 | | |
|----------------------|--------------------|--------------------|---------------------|---------------------|---------------------|
| 21 July– 3 August | 4–17 August | 18–31 August | 1–13 June | 14–28 June | July and August |
| 37 | 22 | 46 | 22 | 13 | 10 |
| 28.1 ± 6.1 (47) | 12.8 ± 3.3 (31) | 26.4 ± 3.5 (36) | 45.3 ± 11.2 (32) | 38.5 ± 11.7 (42) | 28.4 ± 12.2 (33) |
| 26.7 ± 5.5 (45) | 13.5 ± 3.4 (32) | 26.6 ± 3.3 (37) | 40.9 ± 10.6 (29) | 35.3 ± 9.8 (39) | 27.7 ± 11.6 (32) |
| 6.0 ± 1.8 (10) | 8.6 ± 2.7 (21) | 11.0 ± 2.3 (15) | 33.4 ± 12.5 (23) | 16.1 ± 6.9 (18) | 19.3 ± 9.0 (22) |
| 23.6 ± 4.5 (40) | 17.4 ± 5.7 (42) | 30.3 ± 6.2 (42) | 31.5 ± 10.3 (22) | 24.6 ± 16.9 (27) | 23.4 ± 8.9 (27) |
| 1.5 ± 0.7 (3) | 0.6 ± 0.5 (1) | 1.7 ± 0.7 (2) | 27.7 ± 10.6 (19) | 9.0 ± 8.4 (10) | 3.0 ± 2.0 (3) |
| 0.7 ± 0.5 (1) | 0.8 ± 0.6 (2) | 2.8 ± 1.3 (4) | 7.1 ± 3.1 (5) | 3.3 ± 3.3 (4) | 12.2 ± 9.7 (14) |
| 0.9 ± 0.5 (2) | 0.6 ± 0.4 (1) | 0.3 ± 0.2 (0) | 1.8 ± 0.9 (1) | 2.4 ± 1.8 (3) | 0 (0) |
| 0 (0) | 0 (0) | 0.1 ± 0.1 (0) | 0 (0) | 0.1 ± 0.1 (0) | 1.6 ± 1.0 (2) |
| 59.4 ± 6.6 | 41.9 ± 5.5 | 72.8 ± 6.0 | 142.3 ± 11.2 | 90.8 ± 20.1 | 87.3 ± 17.7 |

Impact on the lemming population.—On study grids in 1990, hawks killed at least seven adult lemmings (10% of all adults), and 17 adult lemmings (33%) in 1991. Extrapolating from the 36.6 ha of lemming habitat on grids, we estimate that hawks removed 234 adults from the coastal zone in 1990 and 568 in 1991. The remainder of their estimated summer kill (77 in 1990, 99 in 1991) was from the inland area, giving a total hunting area of 26.25 km² in 1990 and 24.17 km² in 1991.

In 1990, this hunting range included 1626 ha of good habitat, and lemmings weaned 0.38 litters/ha of habitat. With a litter size of five, this converts to 3089 weanlings available, of which hawks consumed an estimated 657 (21.3%) (Table 10). In 1991, hawk hunting range encompassed 1437 ha of good habitat, and lemmings weaned 0.19 litters/ha of habitat. This converts to 1365 weanlings available, of which hawks consumed an estimated 864 (63.3%).

Hawks tended to take more males than females, based on deaths of radio-collared adults (Table 2). Sex ratio data from pellets were limited and showed no clear trend: 1 male:2 females in 1990 and 3:1 in 1991.

Functional response.—The rate at which adult hawks ingest adult lemmings generally increased with increasing adult lemming density (Table 10, Fig. 4), but a linear model did not explain a significant proportion of the variance ($y = 0.429 + 0.486x$; $r^2 = 0.35$; $F = 2.745$; $df = 1, 5$; $P = 0.158$). No other meaningful relationship clearly fits the data (Fig. 4).

The poor fit may, in part, result from inaccurate data. We lacked accurate estimates of lemming density in the pre-incubation period (May), but used the highest density in early June to represent this period (two data points with the highest densities in Fig. 4). The 1992 pre-incubation data point was plotted at the mean density on study grids, which may have underestimated regional densities. Across the range of lemming den-

TABLE 6. Biomass (g, mean ± 1 SE) per scat for juvenile red fox, and percentage of total biomass (in parentheses) of principal prey groups. All biomass estimations are based on conversions of all prey remains, except for *Dicrostonyx*^a, which is based on hair alone. *N* is the sample size of scats.

| Prey type | 1991 | | | |
|---------------------------------|-----------------|-----------------|--------------------|-----------------|
| | 1990 July | 2–22 June | 23 June– 6 July | 7–20 July |
| <i>N</i> | 17 | 21 | 25 | 22 |
| <i>Dicrostonyx</i> ^a | 33.5 ± 5.0 (65) | 25.5 ± 2.6 (69) | 24.5 ± 3.3 (57) | 18.8 ± 4.3 (46) |
| <i>Dicrostonyx</i> ^b | 34.9 ± 5.5 (68) | 27.5 ± 2.6 (74) | 26.0 ± 3.4 (60) | 19.9 ± 4.4 (50) |
| <i>Microtus</i> | 2.3 ± 2.3 (4) | 3.5 ± 1.9 (9) | 2.2 ± 1.2 (5) | 6.1 ± 2.6 (15) |
| <i>Spermophilus</i> | 6.6 ± 4.3 (13) | 5.6 ± 2.8 (15) | 11.9 ± 3.7 (28) | 10.2 ± 3.1 (26) |
| Large mammal | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Large bird | 3.9 ± 3.6 (8) | 0.6 ± 0.4 (2) | 0 (0) | 1.9 ± 1.0 (5) |
| Small bird | 3.7 ± 3.7 (7) | 0 (0) | 3.1 ± 2.2 (7) | 1.4 ± 1.1 (4) |
| Egg | 0 (0) | <0.1 (0) | 0 (0) | 0 (0) |
| Total | 51.5 ± 6.8 | 37.2 ± 3.8 | 43.1 ± 3.2 | 39.5 ± 3.5 |

TABLE 7. Adult and juvenile red fox biomass consumption (from defecation rates) converted to per capita consumption rate of adult and subadult *Dicrostonyx* eaten per summer. To calculate total consumption by the fox population in June, we cut per capita daily consumption by juvenile foxes in half because they are not fully weaned until late June.

| Variable | 1990 | | | 1991 | | | |
|--|-------|-------|-------|----------|--------------|----------|--------------|
| | Jun | Jul | Aug | 2-22 Jun | 23 Jun-6 Jul | 7-20 Jul | 21 Jul-3 Aug |
| Consumption rate | | | | | | | |
| Adult foxes | | | | | | | |
| <i>Dicrostonyx</i> (g/d) | 473.2 | 253.4 | 240.1 | 560.0 | 203.0 | 210.0 | 160.2 |
| Total intake (g/d) | 593.6 | 623.7 | 572.6 | 832.3 | 525.7 | 421.2 | 356.4 |
| Juvenile foxes | | | | | | | |
| <i>Dicrostonyx</i> (g/d) | 192.5 | 244.3 | | 192.5 | 182.0 | 119.4 | |
| Total intake (g/d) | 260.4 | 360.5 | | 260.4 | 301.7 | 237.0 | |
| No. adult : subadult lemmings in scats | | | | | | | |
| | 3:1 | 3:5 | 3:10 | 8:6 | 4:4 | 3:7 | 3:8 |
| <i>Dicrostonyx</i> live mass | | | | | | | |
| Adult lemmings | | | | | | | |
| Mean (g) | 50.0 | 47.9 | 43.1 | 50.3 | 46.5 | 46.7 | 44.1 |
| 1 SE (g) | 1.57 | 1.48 | 1.57 | 1.53 | 2.36 | 2.58 | 2.07 |
| Subadult lemmings | | | | | | | |
| Mean (g) | 29.4 | 19.5 | 19.6 | 29.1 | 22.2 | 22.2 | 22.2 |
| 1 SE (g) | 0.69 | 2.39 | 1.21 | 0.76 | 1.18 | 1.18 | 1.18 |
| <i>Dicrostonyx</i> eaten (no.·d ⁻¹ ·fox ⁻¹) | | | | | | | |
| Adult foxes | | | | | | | |
| Adult lemmings | 7.9 | 3.1 | 2.2 | 7.8 | 3.0 | 2.1 | 1.6 |
| Subadult lemmings | 2.6 | 5.3 | 7.3 | 5.8 | 3.0 | 5.0 | 4.2 |
| Juvenile foxes | | | | | | | |
| Adult lemmings | 3.2 | 3.0 | | 2.7 | 2.6 | 1.2 | |
| Subadult lemmings | 1.1 | 5.1 | | 2.0 | 2.6 | 2.8 | |
| No. adult foxes | 2 | 2 | 5 | 3 | 3 | 3 | 5 |
| No. juvenile foxes | 3 | 3 | | 5 | 3 | 3 | |
| Total <i>Dicrostonyx</i> eaten (no./d) | | | | | | | |
| Adult lemmings | 20.6 | 15.2 | 11.0 | 30.2 | 16.8 | 9.9 | 8.0 |
| Subadult lemmings | 8.5 | 25.9 | 36.5 | 22.4 | 16.8 | 23.4 | 21.0 |
| <i>Dicrostonyx</i> killed (no. per summer) | | | | | | | |
| Adult lemmings | 1430 | | | 1239 | | | |
| Subadult lemmings | 2189 | | | 1852 | | | |

sities observed, the hawks did not increase their kill rates as fast as did foxes (Fig. 3), indicating that hawks are less flexible in their responses to lemming abundance.

In summary, Rough-legged Hawks acted as specialists, being unable to compensate for declining lemming abundance.

Diets of other raptors

Lemmings comprised a substantial percentage, on a frequency of occurrence basis, of the diet of all other raptors and gulls at Pearce Point (Tables 9 and 11), although they were not the dominant prey of these predators, with the possible exception of gulls. The incidence of lemmings in pellets generally declined with declining lemming densities. However, even in summer 1992, when lemmings were rare, they were still remarkably common in gull and Peregrine Falcon diets (see also Table 2). Although much of the gull diet may have been scavenged, we think that lemmings were primary gull prey, since no other predator left lemming parts available to be scavenged.

We lacked data for all these predators on casting rates

and frequency of ingestion of lemming heads, so we could not accurately estimate total impact. However, the incidence of individual lemmings in pellets (Table 12) indicated relatively heavy predation on lemmings by gulls and Peregrine Falcons, and continued predation by these species in 1992, when lemmings were scarce. Casting rate for peregrines, as with other falcons (Balgooyen 1971, Duke et al. 1976), is probably near one pellet per day. If we assume that Peregrine Falcons ingested all lemming heads, the number of lemmings per pellet (Table 12) was particularly high in early summer, reaching 77% of the incidence in Rough-legged Hawk pellets in prelaying period 1991 (Table 10), and was considerably lower in late summer. Each adult Peregrine continued to eat one lemming every 1-2 wk in 1992.

DISCUSSION

Generalist predator hypothesis

The generalist predator hypothesis predicts that lemming numbers remain relatively constant because (1) dominant predators do not respond numerically to lemming density; (2) declining lemming biomass in the

TABLE 7. Continued.

| 1991 | | 1992 | | |
|----------|-----------|----------|-----------|-----------|
| 4-17 Aug | 18-31 Aug | 1-13 Jun | 14-28 Jun | Jul + Aug |
| 81.0 | 159.6 | 163.6 | 141.2 | 110.8 |
| 251.4 | 436.8 | 569.2 | 363.2 | 349.2 |
| 1:5 | 4:17 | 2:3 | 3:3 | 0:2 |
| 44.3 | 41.0 | 50.0 | 46.5 | 47.9 |
| 4.36 | 2.17 | 1.57 | 2.36 | 7.70 |
| 22.2 | 22.2 | 29.4 | 22.2 | 19.5 |
| 1.18 | 1.18 | 0.69 | 1.18 | 2.39 |
| 0.5 | 1.2 | 1.7 | 2.1 | 0 |
| 2.5 | 5.0 | 2.6 | 2.1 | 5.7 |
| 5 | 5 | 3 | 3 | 1 |
| 2.5 | 6.0 | 5.1 | 6.3 | 0 |
| 12.5 | 25.0 | 7.8 | 6.3 | 5.7 |
| | | 171 | | |
| | | 565 | | |

diet is compensated for by increased consumption of alternative prey; (3) predator functional responses are type III; and (4) predators consume very few lemmings at low lemming densities. Our data do not consistently support the generalist predator hypothesis as an explanation for the constancy of lemming densities at Pearce Point. Some predictions were satisfied for some predators, but all predictions were never satisfied for any one predator.

Rough-legged Hawks act as lemming specialists. When lemmings are very rare in spring, the hawks do not nest; in other summers, they are unable to compensate fully for declining lemming consumption by eating alternative prey. Other studies also show that Rough-legged Hawks on arctic tundra eat mainly small rodents, with various birds (principally passerines) and arctic ground squirrels comprising a minor part of the diet (White and Cade 1971, Springer 1975, Smith 1987, Popanov 1988). Rough-legged Hawks also show rapid numerical responses to fluctuating densities of other microtines (White and Cade 1971, Poole and Bromley 1988), so they can be considered nomadic specialists (Galushin 1974).

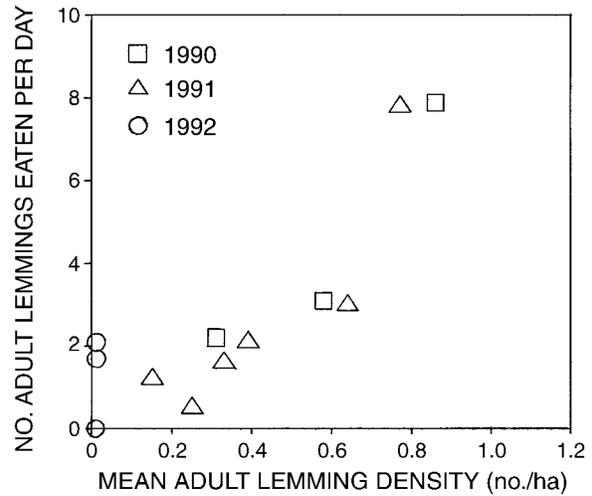


FIG. 3. Functional response of adult red foxes to the density of adult collared lemmings. Data plotted are the number of adult lemmings ingested per day by each adult fox to feed itself for each of the time periods in Table 4.

Red foxes are semigeneralists. In some summers, they can compensate for declining lemming consumption with alternative prey, and they exhibit some features of a type-III functional response. However, foxes still rely primarily on lemmings, especially in spring, and fail to breed successfully when lemming densities are very low in spring. We know of no comparable study of red fox on arctic tundra.

The other raptors, Peregrine Falcons, Gyrfalcons, and Golden Eagles, act as generalists. Lemmings are not their principal prey, so they show little or no numerical response to lemming density, and are able to compensate for declining lemming availability by increased use of their principal prey. We do not know their functional response to changing lemming abundance. Previous studies of tundra raptors have shown

TABLE 8. Conditions and results of the captive feeding experiment with a Rough-legged Hawk, including percentage of lemmings recovered in pellets and pellet casting rate.

| Variable | First period | Second period |
|----------------------------------|--------------|---------------|
| Feeding rate | | |
| No. lemmings eaten/d | 2 | 4 |
| Mass of lemmings eaten | | |
| Mean (g/d) | 74.0 | 136.5 |
| 1 SE (g/d) | 2.0 | 6.23 |
| Hawk body mass | | |
| Start of period (kg) | 1.340 | 1.325 |
| End of period (kg) | 1.325 | 1.505 |
| Period duration (d) | 7 | 12 |
| No. pellets cast | 6 | 13 |
| No. lemmings recovered | 11 of 14 | 39 of 40 |
| Percentage of lemmings recovered | 79 | 98 |
| No. lemmings per pellet | | |
| Mean | 1.83 | 3.00 |
| 1 SE | 0.31 | 0.42 |
| Casting rate (no. pellets/d) | 0.9 | 1.1 |

TABLE 9. Percentage frequency of occurrence of all items in Rough-legged Hawk and Peregrine Falcon (in parentheses) pellets. *N* is the sample size of pellets.

| Prey type | 1990 | | | 1991 | | | 1992 | | |
|---------------------|------------------------------|-----------------------|----------------------|------------------------------|-----------------------|----------------------|------------------------------|------------------------|----------------------|
| | Before incubation (to 9 Jun) | Incubation (to 7 Jul) | Nestling (to 25 Aug) | Before incubation (to 1 Jun) | Incubation (to 5 Jul) | Nestling (to 15 Aug) | Before incubation (to 3 Jun) | Incubation (to 15 Jul) | Nestling (to 30 Aug) |
| <i>N</i> | 13 (3) | 92 (28) | 62 (40) | 42 (10) | 24 (28) | 31 (18) | 8 (13) | 7 (22) | 0 (50) |
| Mammalia | | | | | | | | | |
| <i>Dicrostonyx</i> | 100 (67) | 98 (43) | 82 (25) | 95 (80) | 96 (14) | 100 (33) | 100 (23) | 86 (14) | (16) |
| <i>Microtus</i> | 0 (0) | 13 (7) | 13 (13) | 10 (0) | 17 (0) | 23 (0) | 13 (0) | 29 (5) | (4) |
| <i>Spermophilus</i> | 0 (0) | 1 (0) | 26 (10) | 0 (0) | 0 (0) | 13 (17) | 0 (0) | 14 (0) | (4) |
| Unidentified | 0 (0) | 0 (4) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 0 (0) | (0) |
| Aves | | | | | | | | | |
| Anseriform | 7 (0) | 2 (21) | 5 (13) | 0 (20) | 0 (32) | 0 (6) | 0 (15) | 0 (18) | (26) |
| Charadriiform/ | | | | | | | | | |
| Passeriform | 0 (100) | 8 (46) | 18 (78) | 2 (50) | 13 (71) | 32 (78) | 0 (92) | 0 (77) | (84) |
| Unidentified | 0 (0) | 1 (11) | 2 (0) | 2 (10) | 0 (0) | 6 (6) | 0 (0) | 0 (5) | (0) |
| Insecta | 0 (0) | 0 (0) | 2 (0) | 2 (0) | 4 (4) | 3 (0) | 0 (0) | 0 (0) | (2) |
| Vegetation | 0 (0) | 22 (25) | 40 (15) | 64 (60) | 88 (61) | 74 (50) | 13 (8) | 14 (41) | (12) |
| Sand/pebbles | 0 (0) | 13 (43) | 68 (65) | 39 (60) | 38 (61) | 45 (44) | 100 (100) | 100 (100) | (100) |

little or no use of microtine rodents by Gyrfalcons (White and Cade 1971, Poole and Boag 1988), Peregrine Falcons (White and Cade 1971, Hunter et al. 1988), or Golden Eagles (Poole and Bromley 1988). Our results are unusual, especially for Peregrine Falcons. We estimated diet from pellets, but White and Cade (1971) and Hunter et al. (1988) estimated diet from prey remains at nests. The latter method tends to underestimate the contribution of small mammals to raptor diets, because the entire carcass is often ingested or small bones are lost in the nest structure (Marti 1987, Simmons et al. 1991). This might partly explain the paucity of lemming remains in Peregrine Falcon diets previously reported. The Gyrfalcons' heavy use of ground squirrels probably reflects a regional scarcity of Rock Ptarmigan (*Lagopus mutus*) in summer. Glaucous Gulls may be lemming specialists.

Ermine are thought of as microtine specialists, yet they breed at very low lemming densities at Pearce Point, and probably survive by foraging widely and taking some birds (see also Simms 1978). Grizzly bears and arctic ground squirrels probably function as generalists since they are largely herbivorous and, in the case of bears, consume many ground squirrels (Pearson 1975).

Only Gyrfalcons and Golden Eagles satisfied the prediction (Rosenzweig and MacArthur 1963) that predation on lemmings will be rare at very low lemming densities because of low capture efficiency. Lemmings lack secure hiding places, especially from mammalian predators that dig to reach adults and juveniles in shallow burrows above permafrost. When above ground, lemmings have little cover. This lack of a secure refuge allows predators to drive lemmings to such low densities.

Rosenzweig and MacArthur (1963) also predicted

that, in a system with constant prey, predator populations should be limited by factors other than food, and probably by territoriality. However, at Pearce Point, Rough-legged Hawks and red foxes appeared to be food limited, and there was little evidence of territoriality. Nest abandonment by hawks and fox pup mortality coincided with the rapid decline of lemmings in late June and July. The total daily consumption fell below maintenance levels for adult hawks in late summer, and for foxes in summer 1991. Rough-legged Hawks are apparently food limited in central arctic Canada, with numbers of successful nests and mean brood sizes correlated with microtine prey abundance (Poole and Boag 1988, Poole and Bromley 1988). Red foxes appear food limited in northern portions of their range in Sweden, especially when microtine abundance is low (Englund 1970, Lindström 1989). Rough-legged Hawks and Peregrine Falcons were aggressive towards one another when establishing nests in spring, but their hunting ranges appeared to overlap considerably. Red foxes regularly hunted throughout the hunting ranges of all raptors, and ground squirrels were distributed throughout the study area. Consequently, there was probably substantial competition between predators for the declining prey base of lemmings.

Procedures

Determination of predator diets and impact depends on numerous assumptions that might bias results, and we discuss the most important ones. First, we used 28 as the factor to convert undigested lemming remains in fox scats to an estimate of biomass consumed. This choice was validated by the very similar estimates derived from another method, conversion of the mass of lemming hair in scats. Second, we assumed that the conversion factor does not change with fox age or de-

TABLE 10. Conversion of *Dicrostonyx* remains in Rough-legged Hawk pellets to (A) rates of lemming consumption and (B) lemming biomass consumed by adult hawks during the principal time periods of the study. Period I is before incubation, period II is during incubation, and period III is the nestling stage.

| Variable | 1990 | | | 1991 | | | 1992 |
|--|-----------------|------------------|--------------------|-----------------|------------------|--------------------|-----------------|
| | I (to 9 Jun) | II (to 7 Jul) | III (to 25 Aug) | I (to 1 Jun) | II (to 5 Jul) | III (to 15 Aug) | I (to 9 Jun) |
| A) Consumption rate | | | | | | | |
| Conversion to no. lemmings eaten/d | | | | | | | |
| No. individual remains per pellet | | | | | | | |
| Mean | 2.15 | 1.97 | 1.29 | 1.81 | 2.17 | 1.84 | 1.38 |
| 1 SE | 0.25 | 0.12 | 0.17 | 0.18 | 0.26 | 0.23 | 0.36 |
| Correction factor [†] | 1.02 | 1.27 | 1.27 | 1.02 | 1.27 | 1.27 | 1.27 |
| Mean no. individuals ingested per pellet | 2.19 | 2.50 | 1.64 | 1.85 | 2.76 | 2.34 | 1.75 |
| Casting rate (no. pellets/d) | 1.1 | 0.9 | 0.9 | 1.1 | 0.9 | 0.9 | 0.9 |
| Mean no. individuals ingested/d | 2.41 | 2.25 | 1.48 | 2.04 | 2.48 | 2.11 | 1.58 |
| Conversion to rates of lemming consumption | | | | | | | |
| Ratio, adult : subadult lemming remains | 11:8 | 58:44 | 18:23 | 23:19 | 15:6 | 15:14 | 3:3 |
| Corrected ratio [‡] | 32:56 | 168:308 | 52:161 | 66:133 | 43:42 | 43:98 | 9:21 |
| No. adult lemmings ingested/d | 0.88 | 0.79 | 0.36 | 0.68 | 1.25 | 0.64 | 0.47 |
| No. subadult lemmings ingested/d | 1.53 | 1.46 | 1.12 | 1.36 | 1.23 | 1.47 | 1.11 |
| B) Biomass consumed | | | | | | | |
| Conversion to total consumption | | | | | | | |
| No. adult hawks observed | 8 | 8 | 4 | 12 | 12 | 6 | |
| Period of study (d) [§] | 21 (9) | 28 | 49 | 21 (0) | 34 | 41 | |
| Consumption by adult hawks | | | | | | | |
| Total no. adult lemmings eaten | 396 | | | 838 | | | |
| No. adult lemmings eaten in summer | 311 | | | 667 | | | |
| Total no. subadult lemmings eaten | 804 | | | 1207 | | | |
| No subadult lemmings eaten in summer | 657 | | | 864 | | | |
| Conversion to lemming biomass ingested | | | | | | | |
| Mean adult mass (g) | 50.0 | 50.0 | 47.0 | 50.3 | 49.5 | 44.4 | 50.3 |
| 1 SE adult lemming mass (g) | 1.57 | 1.57 | 1.28 | 1.53 | 1.31 | 1.39 | 1.53 |
| Mean subadult lemming mass (g) | 29.4 | 29.4 | 19.3 | 29.1 | 25.4 | 23.7 | 29.1 |
| 1 SE subadult lemming mass (g) | 0.69 | 0.69 | 1.06 | 0.76 | 1.41 | 1.20 | 0.76 |
| Adult biomass ingested (g/d) | 44.0 | 39.5 | 16.9 | 34.2 | 61.9 | 28.4 | 23.6 |
| Subadult biomass ingested (g/d) | 45.0 | 42.9 | 21.6 | 39.6 | 31.2 | 34.8 | 32.3 |
| Total biomass ingested (g/d) | 89.0 | 82.4 | 38.5 | 73.8 | 93.1 | 63.2 | 55.9 |

[†] To correct for proportion of ingested individuals recognizable in pellets (1.02 when well fed; 1.27 when food stressed).

[‡] To correct for differential digestion of adult and subadult jaws (34.6% adult jaws recovered; 14.3% subadult jaws recovered).

[§] Pre-incubation period is approximate and based on data in Poole and Bromley (1988). Figures in parentheses refer to no. days in June used to calculate the summer (June, July, and August) consumption.

gree of satiation, but juvenile and well-fed foxes digest food less completely (Lockie 1959, Reynolds and Aebischer 1991). Consequently, we may have overestimated consumption rates for juvenile foxes and for foxes in early June. We have no way of correcting this. In most time periods, the estimated daily consumption fell within or close to the range of estimated daily requirements: 320–380 g/d for captive foxes (Lockie 1959, Sargeant 1978) and 450–550 g/d for more active, free-ranging foxes (Scott 1941, Ryszkowski et al. 1973). Estimated daily consumption was particularly high in early June, perhaps in part because of this bias; this was the only time foxes cached lemmings, suggesting that they were satiated. However, lemmings were also more vulnerable at this time, as snow melt removed cover and most burrows were flooded. Foxes

may have increased their intake in early summer to recover body condition after winter.

Third, we assumed that the proportion of adult to subadult lemming remains in fox scats represented the proportions ingested. This is the most problematic assumption. Foxes partly digest bone. Thinner subadult lemming bones are probably better digested, as we observed when feeding lemmings to a captive hawk. Consequently, we probably overestimated the consumption of adult lemmings and underestimated that of subadults, but to an unknown degree.

Fourth, estimates of total impact on the regional lemming population were derived by extrapolating observed mortality rates from study grids, which were small compared to foraging ranges of predators. Grids were 1–4 km from the fox den, and experienced a wide

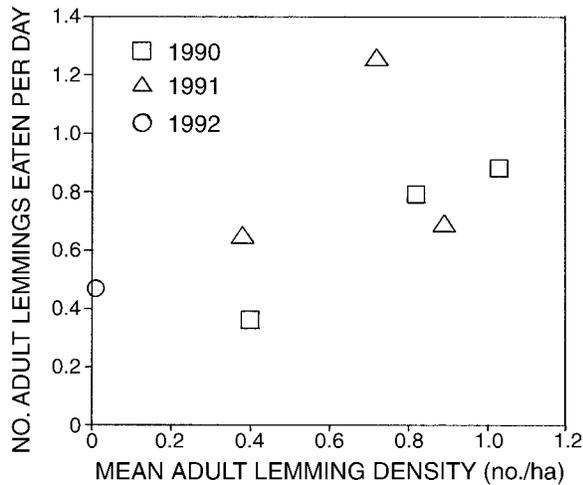


FIG. 4. Functional response of adult Rough-legged Hawks to the density of adult collared lemmings. Data plotted are for pre-incubation periods in each year and incubation and nestling periods in two years (1990 and 1991) (Table 10) and represent the number of adult lemmings ingested by an adult hawk to feed itself.

range of rates of predation by foxes. This gives confidence that regional fox predation rates were within the observed range. However, one grid was <500 m from a hawk nest in 1990, and immediately adjacent to a nest in 1991. Hawk predation rates from grids may have overestimated regional rates, so we may have underestimated the area used by hunting hawks.

Impact on the lemming population

We lacked data on the predators' hunting ranges, but estimated the areas required by foxes, to consume the

adult lemmings in their scats, as 35.8 km² in 1990 and 133.3 km² in 1991. The largest home range record for red fox in North America, in an alpine tundra habitat in northern British Columbia, is 34 km² (Jones and Theberge 1982, Voigt 1987). We frequently observed foxes travelling throughout the 40-km² study area. The natal den was only 1 km from the edge of this area, so foxes undoubtedly used an even larger area for hunting. Although estimates of hunting ranges may have been too large, because of potential biases in scat analyses, they are close to reported values and to our direct observations of area used, so they appear reasonable.

All hawks together needed ≥ 24 –27 km² to satisfy observed kill rates. These estimates seem reasonable, given that one pair of Rough-legged Hawks in the northern taiga of Finland used a 10-km² foraging range to feed nestlings in partially forested bog habitats (Pasanen and Sulkava 1971).

Recruitment of summer-born lemmings as adults on control grids accessible to predators was very low (0.12–0.21 individuals/ha) during summer, despite continuous breeding (Reid et al. 1995). Recruitment was still low in a predator enclosure (0.44 individuals/ha), despite continuous breeding, because most weaned juveniles emigrated from the enclosure (Reid et al. 1995). All grids were within the foraging ranges of hawks and foxes, so subadults on control grids were probably killed at nearly the rates estimated: a combined 68% for the two predators in 1990, and a combined 81% in 1991. The various other predators also could have consumed many subadults. These data confirm our contention that most subadult lemmings were preyed on before maturing, and that the lemming population in the predator enclosure did not grow because

TABLE 11. Percentage frequency of occurrence of prey items in pellets of Gyrfalcons, gulls, and Golden Eagles, before laying (I), during incubation (II), and during the nestling stage (III). Dates are as in Table 9.

| Prey type | Gyrfalcon | | | | | Gull | | | | | Golden Eagle | |
|-------------------------------|-----------|-----|------|----|-----|------|----|-----|------|----------|--------------|------|
| | 1990 | | 1992 | | | 1991 | | | 1992 | | 1991 | 1992 |
| | II | III | I | II | III | I | II | III | I | II + III | All | All |
| <i>N</i> | 22 | 7 | 4 | 15 | 14 | 13 | 20 | 9 | 11 | 7 | 19 | 7 |
| Mammalia | | | | | | | | | | | | |
| <i>Dicrostonyx</i> | 55 | 43 | 0 | 7 | 0 | 69 | 70 | 11 | 36 | 43 | 32 | 0 |
| <i>Microtus</i> | 0 | 0 | 25 | 0 | 0 | 0 | 5 | 0 | 9 | 0 | 0 | 0 |
| <i>Spermophilus</i> | 23 | 0 | 0 | 53 | 71 | 23 | 30 | 11 | 18 | 0 | 95 | 86 |
| <i>Rangifer</i> | 0 | 0 | 0 | 0 | 0 | 23 | 0 | 11 | 0 | 0 | 0 | 0 |
| <i>Vulpes</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 14 |
| Aves | | | | | | | | | | | | |
| Anseriform | 9 | 29 | 0 | 27 | 7 | 23 | 30 | 22 | 9 | 14 | 16 | 14 |
| Galliform | 41 | 14 | 100 | 13 | 7 | 0 | 5 | 0 | 27 | 0 | 0 | 0 |
| Charadriiform/ Passeriform | 5 | 14 | 0 | 7 | 36 | 0 | 10 | 22 | 18 | 0 | 11 | 0 |
| Eggshell | 0 | 14 | 0 | 0 | 0 | 0 | 15 | 11 | 18 | 71 | 0 | 0 |
| Unidentified | 5 | 14 | 0 | 7 | 14 | 15 | 10 | 11 | 9 | 29 | 16 | 0 |
| Insecta (Coleoptera) | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 21 | 43 |
| Echinodermata/Mollusca | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 33 | 0 | 0 | 0 | 0 |
| Crustacea | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 11 | 9 | 14 | 0 | 0 |

TABLE 12. Number of individual lemming remains per pellet (mean, with 1 SE in parentheses), based on molar teeth, for avian predators (other than Rough-legged Hawks) during pre-incubation (I), incubation (II), and nestling (III) periods. Sample sizes are as in Tables 9 and 11. Blank cells indicate no pellets collected, except that all periods are lumped for eagles, and periods II and III are lumped for gulls in 1992.

| Predator | 1990 | | | 1991 | | | 1992 | | |
|------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|-----------------|
| | I | II | III | I | II | III | I | II | III |
| Peregrine Falcon | 0.67 (0.33) | 0.54 (0.15) | 0.20 (0.08) | 1.40 (0.45) | 0.07 (0.05) | 0.22 (0.13) | 0.15 (0.11) | 0.14 (0.10) | 0.06 ± 3 |
| Gyrfalcon | | 0.32 (0.14) | 0.57 (0.30) | | | | 0 | 0.07 (0.07) | 0 |
| Golden Eagle | | | | | | 0.47 (0.26) | | | 0 |
| Gull | | | | 1.08 (0.26) | 1.25 (0.29) | 0.11 (0.11) | 0.36 (0.20) | 0.43 (0.20) | |

most potential immigrating recruits were killed (Reid et al. 1995).

Individual foxes limit population growth of lemmings much more than do individual Rough-legged Hawks, because of their higher daily food needs and their tendency to take more females than males (see also Brooks 1993 and Krebs et al. 1995). Predation on female lemmings removes not only current adults, but also the litters currently suckling and in utero.

The specialist-generalist continuum

The generalist predator hypothesis best explains some European systems. Microtine populations tend to be noncyclic in southern Fennoscandia (south of 60° N), where the rodents belong to a diverse community of herbivores supporting a number of generalist predators, principally the red fox and the Common Buzzard (*Buteo buteo*). Winter snow is not deep enough to prevent successful hunting by these predators (Hansson and Henttonen 1985, 1988). In one such community in southern Sweden, Erlinge et al. (1983, 1984) and Erlinge (1987) demonstrated that predation is the principal factor limiting small-rodent population growth. Generalist predators showed strong functional responses to rodent densities by switching with short time delay from their principal prey, the rabbit (*Oryctolagus cuniculus*), to rodents, when rodents were particularly vulnerable and abundant. The numbers of generalist predators were limited by territoriality. Erlinge (1987) concluded that the conditions of Rosenzweig and MacArthur (1963) were met in this system.

Korpimäki and Norrdahl (1989, 1991a, b) tested the nomadic predator hypothesis with cyclic microtine rodents in western Finland. Some raptors, whose principal foods were microtine rodents, showed rapid numerical responses to microtine densities and strong type-I or type-II functional responses to rodent density (Korpimäki and Norrdahl 1989, 1991a). They may have dampened the amplitude of the cycle by slowing disruptive population growth, but the rodents still fluctuated cyclically; raptors alone were insufficient to stabilize prey densities. Rosenzweig and MacArthur's (1963) conditions were not assessed for all predators,

but probably did not hold for these raptors, which were weakly territorial (Korpimäki and Norrdahl 1991a).

Specialist mustelid predators, most notably the least weasel (*Mustela nivalis*), are the dominant small-rodent predators in a number of communities where rodents fluctuate cyclically. Their strong, but delayed, numerical responses to high rodent numbers, their total reliance on rodent prey in winter, and their adaptations for hunting rodents in burrows allow them to drive the rodents to densities too low for continued support of the predators (Fitzgerald 1977, Korpimäki et al. 1991, Korpimäki 1993).

The diet and numerical responses of red fox at Pearce Point were superficially similar to those in some boreal systems where foxes are semigeneralists. In these regions, red foxes preferentially prey on small rodents, but cannot fully compensate for declining vole consumption, with alternative hare and grouse prey. However, voles in these systems are cyclic. The observed declines in alternative prey appear to result from prey-switching by foxes (alternative prey hypothesis) (Keith 1974, Angelstam et al. 1984, Lindström et al. 1987).

The relative constancy of lemming densities at Pearce Point provides another variant on the specialist-generalist spectrum, and appears to be the result of counteracting seasonal processes. In summer, the specialist hawks and semigeneralist foxes drive declines in the lemmings, which have no substantial temporal or spatial refuge. The declines reach densities too low for these predators both to successfully breed in the current summer and to initiate breeding in the next spring. In this regard, they are similar to the destabilizing cyclic declines driven by specialists. However, even when these principal predators are absent, because of low lemming densities in spring, the persistent generalist predators (falcons, bears, eagles, and ground squirrels) continue to limit summer populations, thereby curtailing the summer growth that generally precedes a winter irruption. In this regard, Pearce Point exhibits stabilizing features of a system limited by generalists.

The winter dynamics at Pearce Point are driven by different factors. Lemming populations frequently grow in winter, because the hawks (and other raptors)

are migratory and because winter specialist predators such as ermine are uncommon. Ermine never reach high densities, probably because prey densities are consistently low and ermine are vulnerable prey themselves. Most importantly, lemmings breed under the snow each spring and in most winters when snow provides adequate thermal cover (Reid and Krebs 1996). This is critical to their dynamics at Pearce Point, and enables these dynamics to differ from those of voles in the same system (Fig. 1; Krebs et al. 1995) and in Fennoscandia. Winter breeding in Fennoscandian *Microtus*, *Clethrionomys*, and *Lemmus* spp. is generally associated with the increase phase of a population irruption (Hansson 1984, Kaikusalo and Tast 1984). Their relative lack of breeding in other winters is probably destabilizing, because they cannot compensate for continuing winter predation and may decline to densities at which specialist or semigeneralist predators cannot survive. This occurred in winter 1991–1992 at Pearce Point, allowing some microtine population growth in the subsequent summer. Even so, this growth in 1992 was limited by the continued action of generalist predators.

In the southern Swedish system fitting the generalist predator hypothesis, microtines are secondary to rabbits in biomass as prey of the principal predators (Erlinge 1987). However, they are the dominant prey of the principal predators at Pearce Point, where they are more crucial to the survival of the predators. In addition, Pearce Point, with high arctic tundra vegetation, has substantially lower primary production and standing crop of vegetation than the Swedish system studied by Erlinge (1987). Microtines at Pearce Point fluctuate at densities substantially less than those in southern Sweden, probably because of less protective cover and lower food availability.

What allows generalist predators to persist?

Arctic ground squirrels appear to be key to understanding how a diverse semigeneralist and generalist predator community persists at Pearce Point. They are the main alternative prey for red foxes, which probably could not persist without them. They are also a principal prey for generalists such as the Golden Eagle, Gyrfalcon, and grizzly bear. They provide a substantial source of food in late summer for the specialist Rough-legged Hawks and the generalist Peregrine Falcons. They are also lemming predators themselves (Boonstra et al. 1990, Reid et al. 1995). We therefore hypothesize that, without ground squirrels, the system would lose the three generalist predators and the red fox, leaving an underutilized lemming prey base ready for more specialist lemming predators, such as the Rough-legged Hawk, arctic fox (*Alopex lagopus*), and jaegers (*Stercorarius* spp.). Hansson and Henttonen (1985) previously speculated that microtine fluctuations may be dampened in North America by predators shifting to ground squirrels. Our study supports this idea, specifically in that squirrels support generalist and semi-

generalist predators that strongly limit lemming population growth in summer.

Oksanen (1990) suggests that generalist predators could stabilize small rodent dynamics in systems with sufficient productivity to support a diverse prey base. However, annual net aboveground primary production in our system (40 to 55 g/m², Reid 1995) is actually low. Thus, Pearce Point appears anomalous, suggesting that factors limiting the coexistence of small herbivores (i.e., microtines and sciurids), such as postglaciation ability to colonize habitats, local patchiness and diversity of habitats (including burrow sites), and extent of overlap in herbivore diets, may be critical in comparisons of community dynamics at North American tundra sites.

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