POPULATION ECOLOGY OF ARCTIC GROUND SQUIRRELS
IN THE BOREAL FOREST DURING THE DECLINE AND LOW PHASES
OF A SNOWSHOE HARE CYCLE

by

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ABSTRACT

I examined food and predation as factors limiting arctic ground squirrel (Spermophilus parryii plesius) populations during the decline and low phases of a snowshoe hare cycle (1992 - 1995). Food and predator limitation were tested experimentally with large-scale (36-ha) experimental manipulations: two food-supplemented areas, a predator exclosure, and a food-supplemented treatment where predators were also excluded.

Predator removal doubled population density, while addition of food resulted in a four-fold density increase. Removal of predators and addition of food together resulted in a 10-fold increase in arctic ground squirrel population densities. Population densities and adult survival rates were lower in 1992 and 1993 (two years after the snowshoe hare population decline) than in 1994 and 1995. Food supply and predation interact to limit arctic ground squirrel population densities in the boreal forest during the decline and low phases of the snowshoe hare cycle.

Supplemental food did not affect dispersal distances or dispersal frequency of 172 radio-collared juveniles of either sex in any year. Juveniles that moved farther from their natal burrow were more likely to die. Males moved farther than females and died more frequently. Dispersal tendency was unrelated to population density in males. Females increased their tendency to disperse only on a study site with population densities 17x those of control
populations. Male arctic ground squirrels probably disperse to avoid inbreeding, while females may disperse in response to resource limitation at very high densities.

Philopatric females had higher fitness than females that dispersed, particularly if survival during dispersal was taken into account. As population density increased from 1992 - 1995, home range overlap of adult females also increased, as daughters survived to reproductive age in contact with their mother’s home range.

A stage-based simulation model of the annual cycle of activity and hibernation in arctic ground squirrels was strongly sensitive to adult and juvenile female survival. Arctic ground squirrel populations in the boreal forest can sustain a positive rate of population increase during the low phase of the snowshoe hare cycle, facilitated by flexibility of adult female home range overlap and high adult female survival.
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DEDICATION

This thesis is dedicated to my father, Buzz Byrom, who helped shape my intellectual development and who always encouraged me to do my best, because it was good enough for him.
CHAPTER 1: INTRODUCTION

Overview

Ground-dwelling sciurids are particularly tractable species with which to examine the relationship between external factors limiting population growth, and the social structure of the population. In this thesis I investigate the effects of predation and food on arctic ground squirrel (Spermophilus parryii) populations in the Canadian boreal forest. In particular, I consider the influence of these external limiting factors on population density and adult and juvenile survival during the decline and low phases of a snowshoe hare (Lepus americanus) cycle (1992 to 1995). I also consider the survival costs of dispersal and philopatry in juvenile arctic ground squirrels, and measure fitness of philopatric and dispersing juvenile female arctic ground squirrels to examine the implications for the population structure of this species in the boreal forest.

Arctic ground squirrels in the boreal forest community

Much of the range of the arctic ground squirrel is in arctic and alpine tundra regions of Canada, Alaska, and Siberia (Nadler et al. 1974; Nadler and Hoffmann 1977). Three subspecies are found in North America (S. p. parryii, S. p. plesius, and S. p. kennicottii). The Yukon subspecies (S. p. plesius) is the smallest of the three subspecies of arctic ground squirrels. Only the subspecies S. p. plesius
includes the boreal forest of northwestern North America as part of its range (Banfield 1974; Nadler and Hoffmann 1977).

Much of our understanding of the population ecology of the three North American subspecies of the arctic ground squirrel comes from research done in arctic and alpine tundra habitats (Carl 1971; Green 1977; Batzli and Sobaski 1980) or in open meadows (McLean 1982, 1983, 1985; Lacey 1991). Arctic ground squirrels living in the boreal forests of northwestern North America are the third most abundant small herbivore in terms of biomass after red squirrels and snowshoe hares (Krebs et al., unpublished data).

In boreal forest regions, snowshoe hares show regular cyclic fluctuations with a period of 8 - 11 years and up to a 100-fold change in amplitude (Elton and Nicholson 1942; Keith et al. 1977; Krebs et al. 1986). Resident (year-round) predators of the snowshoe hare in boreal forest communities are lynx (*Lynx canadensis*), coyotes (*Canis latrans*), goshawks (*Accipiter gentilis*), and great horned owls (*Bubo virginianus*). In summer, migratory raptors such as red-tailed hawks (*Buteo jamaicensis*) and northern harriers (*Circus cyaneus*) migrate north to breed in the Yukon. During cyclic fluctuations of the snowshoe hare, other herbivores in the community such as the arctic ground squirrel may be indirectly affected by changes in predation intensity (Angelstam et al. 1984; Keith and Cary 1991). However, arctic ground
squirrels hibernate in winter and are thus unavailable to predators for seven to eight months of the year. They provide a pulse of biomass during the summer months, following a period of potential food shortage for winter predators. The impacts of predators on this seasonally abundant prey species as a consequence of the cyclic fluctuation are not well documented.

Arctic ground squirrel populations in the boreal forest have the potential to show population fluctuations in response to the 10-year cycle of snowshoe hares and their predators. Indirect effects of snowshoe hares on other herbivores in the community, such as ground squirrels, are two-fold. Squirrel populations may decline as a result of intensifying predation after the snowshoe hare crash, as predators switch to more abundant species when snowshoe hares become scarce (O'Donoghue 1997). In addition, arctic ground squirrel populations may decline when snowshoe hare populations are high, as a result of competition with snowshoe hares for food (Hubbs 1994). Arctic ground squirrels have similar, although not completely overlapping, food preferences for herbaceous species such as lupins (Lupinus arcticus) and grasses (McLean 1985; Hik 1994). In this thesis I address the indirect effect of predation as an external factor limiting arctic ground squirrel population density and survival of all age-sex classes in the population. Because snowshoe hare population densities peaked in 1989 - 1990 and were low during my study (1992 to 1995) I do not address the question of whether
competition with snowshoe hares influences arctic ground squirrel population trends.

Arctic ground squirrels: annual cycle of activity and hibernation

Arctic ground squirrels are diurnal ground-dwelling sciurid rodents, living in groups of related females and territorial males in a polygynous social structure typical of many ground-dwelling rodents (Armitage 1981, Michener 1983; McLean 1984). Like most North American ground-dwelling sciurids, they are obligate hibernators. Squirrels emerge from a seven- to eight-month hibernation period in early to mid April; males typically emerge one to two weeks before females (Carl 1971; Lacey 1991). Both males and females are reproductively mature upon emergence as yearlings, and mating occurs as soon as females emerge from hibernation. Gestation lasts about 25 days (Lacey 1991). Female arctic ground squirrels normally reproduce every year during adult life (≥ 1 year old), having litters of four to seven offspring (Carl 1971; Green 1977; McLean 1985; Lacey 1991; Hubbs 1994). Juveniles emerge from natal burrows in mid to late June (approximately 28 days after birth). Weaning occurs within one to two weeks after juvenile emergence from the natal burrow, and juveniles disperse two to three weeks after emergence. By early to mid August, most juveniles that survive have finished dispersal and associated exploratory movements and have settled in a permanent location (Green 1977; Lacey 1991; pers. obs.). Adult females
usually begin hibernation in late July to late August; adult males follow shortly thereafter, whereas juveniles require more time to gain weight and may hibernate as late as September or early October.

Study sites: experimental manipulation of predation and food in arctic ground squirrel populations

In this thesis I present results from experimental manipulations of predation and food supply as factors limiting boreal forest populations of arctic ground squirrels in the Shakwak Trench, southwestern Yukon Territory, Canada (61°N, 138°W). The experimental setup was part of the Kluane Boreal Forest Ecosystem Project (Krebs et al. 1992, 1995; Boutin et al. 1995), a 10-year series of experimental manipulations established in 1986 to examine trophic linkages in the boreal forest community. Arctic ground squirrels of this region live in a patchy environment in which large stands of open and closed white spruce (Picea glauca) forest are interspersed with smaller areas of open meadow and shrub-meadow consisting of shrubs such as grey willow (Salix glauca) and bog birch (Betula glandulosa). Herbaceous plants are found in meadows, open spruce, and shrub areas (Douglas 1974). All study sites described below were situated in areas of approximately similar habitat (mostly open spruce and shrub-meadow habitat; Hubbs and Boonstra, in press).
Squirrels were studied on eight 9-ha experimental grids containing 100 grid points spaced 30 m apart and located in a 10x10 array (Figure 1.1): (1) four unmanipulated CONTROL grids (Controls A, B, C, and D); (2) two FOOD-supplemented grids (Food 1 and Food 2) provisioned ad lib with pelleted rabbit chow (minimum 16% crude protein) distributed with a fertiliser spreader along four 600-m cut lines ("feeder rows"); (3) one PREDATOR EXCLOSURE grid, a 1-km$^2$ area surrounded by an 8600-Volt electric fence to exclude large terrestrial mammalian predators, and partially covered by monofilament fishing lines spaced approximately 30 cm apart to deter avian predators; and (4) one PREDATOR EXCLOSURE+FOOD grid which was a 1-km$^2$ area surrounded by an electric fence as above and provisioned as above with pelleted rabbit chow. PREDATOR EXCLOSURE, FOOD, and PREDATOR EXCLOSURE+FOOD treatments were all located within larger (36 ha) experimental treatments established in 1986 to manipulate snowshoe hare populations (Krebs et al. 1992, 1995; Boutin et al. 1995).
FIGURE 1.1. Map of study sites at Kluane in the Shakwak Trench, southwestern Yukon Territory (61°N, 138°W) showing locations of CONTROLS A - D, PREDATOR EXCLOSURE, FOOD, AND PREDATOR EXCLOSURE+FOOD treatments. Researchers were based at the Kluane Lake Research Station, run by the Arctic Institute of North America.
Chapter overview

In Chapter 2 I examine the effects of the cyclic fluctuation of snowshoe hares and their predators on survival of arctic ground squirrels, rates of population change, and population density in the boreal forest during the decline and low phases of a snowshoe hare cycle. I test the hypotheses that predation alone, food alone, or food and predation together limit arctic ground squirrel population density. Predation as a limiting factor has been investigated in several species of ground-dwelling sciurid (e.g., Michener and Michener 1977; Schmutz et al. 1979; Schmutz and Hundle 1989; Elliott and Guetig 1990). In particular, declines in population densities of ground squirrels have been reported following snowshoe hare declines (Erlien and Tester 1984; Adamcik et al. 1979; Keith and Cary 1991), and increased predation intensity on such populations has been suggested as a possible cause.

Few studies have attempted large-scale experimental manipulation to examine the influence of factors such as predation and food supply in limiting populations (Crawley 1992; Carpenter et al. 1995; Krebs et al. 1995). Theoretical evidence (McNamara and Houston 1987; Lima and Dill 1989) and empirical evidence (Dickman 1992; Desy and Batzli 1989; Desy et al. 1990; Hughes et al. 1994; Anholt and Werner 1995; Hik 1995; Krebs et al. 1995) suggest that food supply and predation may act in combination to limit populations. However, the mechanisms by which such an interaction occurs
may differ among taxa (Anholt and Werner 1995). Adult survival, juvenile survival and dispersal, and fecundity may all be influenced by food supply and by presence of predators.

Hubbs (1994) and Hubbs and Boonstra (in press) concluded that food was more important than predators in limiting arctic ground squirrel populations from 1990 to 1992, although food may have also interacted with predation during this time. Karels (1996) found that food-supplementation interacted with predation to influence population density of arctic ground squirrels in the low phase of the snowshoe hare cycle (1993 and 1994). In Chapter 2 I examine the effects of food and predation on arctic ground squirrels in the boreal forest from 1992 to 1995.

In Chapters 3 and 4 I extend our knowledge of arctic ground squirrel population dynamics at Kluane to an understanding of processes of philopatry and dispersal in the juvenile age-class. In Chapter 3 I examine the survival consequences of natal dispersal for male and female juvenile arctic ground squirrels. I use the large-scale experimental manipulations to test the hypothesis that dispersing individuals have high mortality, as has been assumed historically (Lidicker 1975; Gaines and McClenaghan 1980). Radio-collaring individual sciurids with the intention of investigating the survival consequences of dispersal has been tried in only a few cases (e.g., Hackett
1987; Garrett and Franklin 1988; Wiggett et al. 1989; Larsen and Boutin 1994). However, to my knowledge, no studies have attempted to determine the fate of individual dispersers in combination with large-scale predator removal or a combination of food supplementation and predator removal.

I also examine the effects of large-scale addition of food on dispersal movements of juvenile arctic ground squirrels in the boreal forest. Competition for food resources has been advanced as both a proximate and an ultimate cause of natal dispersal in some sciurids (Holekamp 1986). Yet Dunford (1977) found no effect of supplemental food on dispersal of either sex in a round-tailed ground squirrel (S. tereticaudus) population. Dobson (1979) found that young male California ground squirrels (S. beecheyi) did not respond to food addition, whereas young females responded by moving to food supplemented areas. He concluded that young males disperse to avoid inbreeding, whereas young females disperse only if density is high relative to food availability. However, few researchers have manipulated food supply for more than a few months to determine how food supplementation affects natal dispersal in young sciurids.

In Chapter 4 I focus specifically on philopatry and dispersal of juvenile female arctic ground squirrels in the boreal forest. Studies of many ground-dwelling sciurid species have shown that females generally remain philopatric (e.g.,
Michener and Michener 1977; Michener 1979; Holekamp 1984; Wiggett and Boag 1992). Yet the fitness consequences of natal dispersal and philopatry are not well understood because of the difficulties of estimating costs and benefits (both in terms of survival and reproduction) to dispersing and resident individuals (Gaines and McClanahan 1980; Greenwood and Harvey 1982; Stenseth and Lidicker 1992). Dispersal has been described as the “glue” which joins ecology, population genetics, ethology, and evolution (Stenseth and Lidicker 1992). The evolution of philopatry is probably equally significant (Waser and Jones 1983). Quantifying the reproductive consequences of philopatry and dispersal can help in understanding the evolutionary costs and benefits of this continuum of strategies.

In Chapter 5 I present a stage-based simulation model of arctic ground squirrel populations at Kluane, which I used to determine sensitivity of rates of population change to various demographic parameters including active season survival of adults and juveniles of both sexes, and to reproduction and overwinter survival. I conclude by linking juvenile and adult survival, fecundity and dispersal to the observed changes in arctic ground squirrel populations during the cyclic fluctuation of snowshoe hares and their predators in the boreal forest.
**Literature cited**


Hubbs, A. H. 1994. The effects of food and predation on population regulation of the arctic ground squirrel (Spermophilus parryii plesius) during the peak and decline phases of a snowshoe hare cycle. M.Sc. thesis, University of Toronto, Canada.


CHAPTER 2: EXPERIMENTAL MANIPULATION OF PREDATION AND FOOD SUPPLY IN A POPULATION OF ARCTIC GROUND SQUIRRELS IN THE BOREAL FOREST

Introduction

External factors limiting the growth of animal populations have historically attracted much interest (Elton 1927; Andrewartha and Birch 1954; Errington 1967; Boutin 1990; Crawley 1992). Few studies, however, have attempted large-scale experimental manipulation of factors such as predation and food supply (Crawley 1992; Carpenter et al. 1995) to determine their effects on population demography, either singly or in combination. In this paper I address the question of whether arctic ground squirrels (Spermophilus parryii plesius) are limited by food supply, predation, or a combination of food and predation in a boreal forest system with a dominant cyclic herbivore, the snowshoe hare (Lepus americanus).

Snowshoe hares show regular cyclic fluctuations in the North American boreal forest, with a period of 8 - 11 years and up to a 100-fold change in amplitude (Elton and Nicholson 1942; Keith et al. 1977; Boutin et al. 1986; Krebs et al. 1986; Keith 1990). The main predator species resident in the boreal forest are lynx (Lynx canadensis), coyotes (Canis latrans), goshawks (Accipiter gentilis),
and great horned owls \textit{(Bubo virginianus)}. In summer, migratory raptors such as red-tailed hawks \textit{(Buteo jamaicensis)} arrive to breed. During the decline and low phases of the snowshoe hare cycle, arctic ground squirrels in the boreal forests of northwestern North America may become an "alternative prey" (Angelstam \textit{et al.} 1984) during summer months.

Impacts of predators on alternative prey species as a result of a cyclic decline in another herbivore have been observed several times (e.g., Angelstam \textit{et al.} 1984; Sutherland 1988; Marcstrom \textit{et al.} 1989; Keith and Cary 1991; Korpimäki and Norrdahl 1991; Small and Keith 1992). Arctic ground squirrels are the third most abundant prey species in the northwestern boreal forest, after snowshoe hares and red squirrels \textit{(Tamiasciurus hudsonicus)} (Krebs \textit{et al.} 1992a). They are commonly found in arctic and alpine tundra habitats in Canada and Alaska (e.g., Carl 1971; Green 1977; McLean 1985), but a small fraction of their range includes the northwestern boreal forests (Banfield 1974). However, arctic ground squirrels hibernate in winter and are thus unavailable to predators for seven to eight months of the year. They provide a pulse of biomass during the summer months, following a period of potential food shortage for winter predators. The impacts of predators on this seasonally abundant prey species as a consequence of the cyclic fluctuation in snowshoe hares are not well documented.
Predation as a limiting factor has received much attention in the literature. Predators frequently limit and sometimes regulate prey populations (Erlinge et al. 1984; Kidd and Lewis 1987; Sinclair 1989), although in some cases predation has little effect on prey population densities (Newsome 1990; Skogland 1991). Predation as a limiting factor has been investigated or suggested in several species of ground-dwelling sciurids (Michener and Michener 1977; Michener 1979; Schmutz et al. 1979; Erlien and Tester 1984; Schmutz and Hungle 1989; Elliott and Guetig 1990; Murie 1992).

That animal populations are food-limited is also widely accepted (Boutin 1990). Food supplementation has been shown to have dramatic effects on population densities, home range size, recruitment, reproduction, and immigration in small mammal populations (Gilbert and Krebs 1981; Taitt and Krebs 1981; Mares et al. 1982; Boutin 1990; Klenner and Krebs 1991). Ground squirrel populations have also responded to food supplementation. For example, food addition caused dramatic increases in Columbian ground squirrel (S. columbianus) litter sizes, spring body weights, survival of young, and immigration to food-supplemented populations, whereas age at maturity of females decreased (Dobson and Kjelgaard 1985a,b; Dobson 1995). Hubbs and Boonstra (in press) recorded increases in growth rates, body weights, and litter sizes of food-supplemented populations of arctic ground squirrels in the boreal forest at Kluane during the peak and decline phases of the snowshoe hare cycle.
Recent theoretical (McNamara and Houston 1987; Lima and Dill 1989; Abrams 1994) and empirical (e.g., Dickman 1992; Desy and Batzli 1989; Desy et al. 1990; Hughes et al. 1994; Anholt and Werner 1995; Hik 1995; Krebs et al. 1995) evidence suggests that external factors such as food and predation interact to limit populations. In this paper I present results from large-scale experimental manipulations to examine predation and food supply as factors limiting arctic ground squirrel populations in the boreal forest. I concentrate particularly on the effects of these factors on population density, adult and juvenile survival, and population growth rates of arctic ground squirrels during the decline and low phases of a snowshoe hare cycle (1992 to 1995). Hubbs and Boonstra (in press) reported the effects of predation and food on arctic ground squirrel populations during the peak and early decline phases of the snowshoe hare cycle and concluded that food was more important than predators in limiting arctic ground squirrel populations from 1990 to 1992, although food may also have interacted with predators at this time. Karels (1996) found that food supplementation increased adult and juvenile growth rates, body condition, and reproduction, and interacted with predation to affect population densities of arctic ground squirrels in the low phase of the snowshoe hare cycle (1993 to 1994).
I tested three alternative hypotheses to explain arctic ground squirrel population densities and survival in the boreal forest.

**Hypothesis 1:** Arctic ground squirrel populations in the boreal forest are limited by predators ("top-down" hypothesis).

**Prediction 1:** Areas where predators are excluded will have higher densities of ground squirrels than control areas during the decline and low phase of the snowshoe hare cycle.

**Prediction 2:** Arctic ground squirrels on unmanipulated areas will have lower survival rates than squirrels on areas where predators are excluded, as predators concentrate foraging effort on squirrels after the snowshoe hare decline.

**Prediction 3:** As predator numbers decline, densities and population growth rates of arctic ground squirrels will increase during the low and early increase phase of the snowshoe hare cycle.

**Hypothesis 2:** Arctic ground squirrel populations in the boreal forest are food-limited ("bottom-up" hypothesis).

**Prediction 1:** Compared with unmanipulated areas, higher densities will be observed on food-supplemented areas.

**Prediction 2:** Population densities on food-supplemented areas will be similar to an area where predators are excluded and where food is added.
Hypothesis 3: Arctic ground squirrels are limited by both food and predation ("interactive" hypothesis).

(See below for a description of the experimental manipulations).

Prediction 1: Ground squirrel population densities should be ranked in the following order: PREDATOR EXCLOSURE+FOOD > FOOD ≥ PREDATOR EXCLOSURE > CONTROLS.

Prediction 2: Ground squirrel survival should be ranked in the following order: PREDATOR EXCLOSURE+FOOD > FOOD ≥ PREDATOR EXCLOSURE > CONTROLS.
Methods

Study sites

Squirrels were studied on eight 9-ha experimental grids containing 100 grid points spaced 30 m apart and located in a 10×10 array: (1) four were unmanipulated CONTROL grids (Controls A, B, C, and D); (2) two were FOOD-supplemented grids (Food 1 and Food 2) provisioned *ad lib* with pelleted rabbit chow (minimum 16% crude protein) distributed with a fertiliser spreader along four 600-m cut lines ("feeder rows"); (3) one was a PREDATOR EXCLOSURE grid, a 1-km² area surrounded by an 8600-Volt electric fence to exclude large terrestrial mammalian predators, and partially covered by monofilament fishing lines spaced about 30 cm apart to deter avian predators; and (4) one was a PREDATOR EXCLOSURE+FOOD grid which was a 1-km² area surrounded by an electric fence as above, and provisioned with pelleted rabbit chow as above. PREDATOR EXCLOSURE, FOOD, and PREDATOR EXCLOSURE+FOOD treatments were all located within larger (36 ha) experimental treatments established to manipulate snowshoe hare populations (Krebs *et al.* 1992b, 1995; Boutin *et al.* 1995).
Population density and survival

Population density and survival of arctic ground squirrels were monitored for six consecutive years: 1990 to 1995 (data from 1990 to 1992 were collected by A. Hubbs (Hubbs 1994)). Regular trapping occurred throughout the active season, and I censused populations twice per year (see below). Adult squirrels were trapped in Tomahawk live traps (14 x 14 x 40 cm, Tomahawk live trap Co., Tomahawk, Wisconsin) baited with peanut butter, tagged with monel No. 1005-1 tags (National Band and Tag Co., Newport, Kentucky) in both ears, weighed to the nearest 5 g with a Pesola spring scale, sexed, and radio-collared from 1992 to 1995 with 5-g radio collars (PD-2C transmitters, Holohill Systems Limited, Woodlawn, Ontario). Between 13 and 30 adult arctic ground squirrels were radio-collared on each of three experimental treatments, and a total of 13 to 25 radio-collared adult squirrels were distributed among the four controls, from 1992 to 1995.

Squirrels were radio-collared to estimate home range size and active season survival from emergence in April to immersgence in August or September. I located adults twice per week with a hand-held antenna. Home ranges of adult arctic ground squirrels were estimated using the 95% Minimum Convex Polygon (MCP) method (Jennrich and Turner 1969). I used a minimum of 10 fixes for each squirrel, and only squirrels present on the study sites throughout each active season were used to estimate home range sizes.
Juveniles were trapped as soon as they emerged in June and were ear-tagged, weighed, and sexed as described for adults above. One hundred and ninety-five juveniles were radio-collared with 6-g expandable collars (SM-1 transmitters; AVM, California and SS-2 transmitters; Biotrack, Dorset, England; both with Hg-675 batteries) from 1993 to 1995 (see Appendix I for a description of the juvenile radio collars). I located juvenile squirrels at least every two days with a handheld antenna to measure juvenile survival and dispersal (Chapter 3).

**Annual population censuses**

Population densities on each of the experimental treatments and controls were estimated twice each year; once in spring (first two weeks of May) to measure spring densities and overwinter survival, and once in late summer (last two weeks of July) to estimate population densities after reproduction and juvenile dispersal but prior to hibernation. Ground squirrels on PREDATOR EXCLOSURE+FOOD and FOOD treatments usually emerged from hibernation before squirrels on PREDATOR EXCLOSURE and CONTROL treatments, and thus were censused first both in spring and late summer.

*Burrow trapping.* From 1990 to 1992, squirrels were trapped at their burrows. One trap was placed at each burrow entrance, and 2 - 6 traps were placed at large perennial burrow systems with multiple entrances. Traps were set at 0800h and checked twice per morning at 2-hour intervals, and closed at 1200h (Hubbs 1994).
Squirrels were trapped for two consecutive days (to give a total of four trapping sessions), and population densities estimated using program CAPTURE (Otis et al. 1978).

*Stake trapping.* From 1993 to 1995, squirrels were trapped at alternate grid stakes. Traps were set at 0700h, checked three times per morning at 1.5-hour intervals, then closed by 1230h. Captures from the three daily trapping sessions were pooled to give an overall daily capture rate. This procedure was repeated for at least three consecutive days until the standard error was ≤10% of the population estimate for the model selected by program CAPTURE (Otis et al. 1978).

I tested whether the change in trapping method (from burrow trapping in 1990 to 1992 to stake trapping in 1993 to 1995) affected population estimates in the following way. During the spring census in 1993, squirrels on the PREDATOR EXCLOSURE treatment were trapped at burrows (which gave a population estimate of 12±0 (95% C.L.); n=12; program CAPTURE). The same population was trapped at stakes within a few days (which gave a population estimate of 13±0 squirrels). These estimates were similar enough that I assumed that the two methods were comparable. In addition, treatments with high densities of squirrels were trapped at both stakes and burrows to reduce competition for traps.
Population trends and rates of increase

Instantaneous rates of population change were calculated as \( r = \ln \left( \frac{N(t+1)}{N(t)} \right) \); where \( N(t+1) \) is population density at time \( t+1 \), \( N(t) \) is population density at time \( t \), and \( r \) is the instantaneous rate of population change per year (Caughley 1977). Spring population estimates obtained from program CAPTURE (Otis et al. 1978) were used to calculate rates of population change. Estimates of adult and juvenile survival obtained from radio-telemetry on each treatment in each year (Pollock et al. 1989) were also plotted against the \( N(t+1)/N(t) \) ratio (the finite rate of population increase, \( R \)) to determine how survival on all experimental treatments affected rates of population change from year to year.

Concurrent changes in predator and snowshoe hare populations

An index of changes in avian and mammalian predator biomass, arctic ground squirrel biomass and survival, and snowshoe hare biomass was calculated from 1990 to 1995. Mammalian predator biomass was calculated by estimating numbers of lynx and coyotes (O'Donoghue, thesis submitted) in the Shakwak Trench (350 km²) and multiplying by the average body mass of each (9.0 kg for lynx and 10.0 kg for coyotes). Numbers of lynx and coyotes were estimated by radio-collaring as many animals as possible in the Kluane study area and taking weekly locations of collared individuals. The number of individuals within each family group was then determined by track counts in early winter, and this index
was used to determine whether other family groups existed within the 350 km² study area (Boutin et al. 1995; M. O'Donoghue, pers. comm.). Avian predator biomass was calculated by estimating numbers of breeding pairs of raptors (great horned owls, goshawks, and red-tailed hawks) in a 100-km² area and multiplying by the average body mass of each (1.2 kg for goshawks, 1.3 kg for red-tailed hawks, and 1.4 kg for great horned owls). Raptor numbers (pairs of raptors per 100 km²) were estimated using nest searches, playbacks, and telemetry (Doyle and Smith 1994; Boutin et al. 1995; F. Doyle, pers. comm.) within the study area. Snowshoe hare population densities were estimated by mark-recapture in spring (March) and fall (October) on all experimental and control sites in the Kluane study area (Boutin et al. 1995). Snowshoe hare biomass was calculated by multiplying population estimates by the average body mass of a snowshoe hare (1.4 kg).

Statistical analyses

Most statistical comparisons were made using JMP for Macintosh (SAS Institute 1994). Power analyses were calculated with STPLAN (Brown et al. 1993). Survival of adults and juveniles was estimated from formulas in Pollock et al. (1989), modified for use with MS-DOS by C. J. Krebs (Unpublished). All survival estimates were compared using a log-rank test (Pollock et al. 1989). Comparisons of density estimates were made in two ways. Paired t-tests with a Bonferroni correction (Sokal and Rohlf 1995) were done to compare density on
each experimental treatment with the mean density on CONTROLS A - D from 1990 to 1995. Randomised intervention analysis (RIA) (Manly 1991) was also done by W. Hochachka (pers. comm.) to determine whether the trends observed on each of the treatments were greater than would be expected by chance, given the background variation in population size shown by control populations. Randomisations were repeated 5000 times, and the proportion of times that the test mean density exceeded the observed mean density is the one-tailed probability that there is no difference in population size between a treatment and the controls. These tests were chosen over conventional statistical tests such as repeated measures analysis of variance because of the lack of replication on the PREDATOR EXCLOSURE and PREDATOR EXCLOSURE+FOOD treatments. Details of the RIA are given by Karels (1996).
Results

Population density

Population densities of arctic ground squirrels were high in 1990 and 1991, during and immediately after the peak in snowshoe hare numbers (average population density was 2.16 squirrels/ha on CONTROL areas in spring 1991). Densities declined on all treatments to a low of 0.54 squirrels/ha on CONTROL areas in spring 1993, and have thereafter been increasing (Figure 2.1). Population densities on the PREDATOR EXCLOSURE+FOOD treatment reached a peak of 45.6 squirrels/ha in summer 1995.

Differences between population densities on CONTROLS A - D and densities on all three treatments were significant when compared using a paired t-test (Table 2.1). Randomized intervention analysis revealed significant differences in arctic ground squirrel population densities on PREDATOR EXCLOSURE+FOOD and FOOD treatments, but the PREDATOR EXCLOSURE treatment failed to increase arctic ground squirrel population densities significantly by this measure. Population densities of arctic ground squirrels are tabulated in Appendix II, and for controls pooled and for the three treatments, are shown in Figure 2.1. On average, removal of predators doubled arctic ground squirrel population densities, whereas food addition approximately quadrupled population densities.
Population densities increased 10-fold when food was added and predators were removed simultaneously (Figure 2.2).
FIGURE 2.1.  Arctic ground squirrel population density (number of squirrels per hectare, plotted on a logarithmic scale) on four CONTROL grids, two FOOD addition treatments, a PREDATOR EXCLOSURE treatment, and a PREDATOR EXCLOSURE+FOOD treatment, 1990 to 1995. Population densities on control grids are pooled; densities on individual controls (A - D) are listed in Appendix II. Population densities from 1990 to 1992 were estimated by A. Hubbs (Hubbs 1994; Hubbs and Boonstra, in press).
FIGURE 2.2. Ratio of population densities of arctic ground squirrels on each experimental treatment (PREDATOR EXCLOSURE, FOOD 1 and 2, and PREDATOR EXCLOSURE+FOOD) to population densities on CONTROLS A-D pooled, 1990 to 1995. Arrows show the average increase in population density on each experimental treatment, compared with controls.
TABLE 2.1. Results of paired t-tests with Bonferroni correction, and randomized intervention analysis to compare changes in arctic ground squirrel population density on three experimental manipulations and four controls, 1990 to 1995. Sig. = significance. There were 11 degrees of freedom for all t-test comparisons. P.EX = PREDATOR EXCLOSURE.

<table>
<thead>
<tr>
<th></th>
<th>Paired t-test ($\alpha = 0.017$)</th>
<th>Randomization test</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>$t$</td>
<td>$p$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<tr>
<td>CONTROLS VS.</td>
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<tr>
<td>P.EX.</td>
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<td>CONTROLS VS.</td>
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<tr>
<td>FOOD</td>
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<td>CONTROLS VS.</td>
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<tr>
<td>P.EX.+FOOD</td>
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<td></td>
</tr>
</tbody>
</table>

* One-tailed
Survival

Predation was the greatest proximate cause of mortality during the active season for both juvenile and adult arctic ground squirrels from 1993 to 1995 (Appendix III) and accounted for 87% of mortalities among radio-collared adults in 1992 (Hubbs and Boonstra, in press). Most kills from 1993 to 1995 were due to avian predators (75% of known adult kills and 79% of known juvenile kills were by raptors during this time). Predator removal, food addition, and predator removal combined with food addition generally increased survival of radio-collared adults from 1993 to 1995 (Figure 2.3). These differences were not significant, but the power of the test was low (varied from 0.25 - 0.60) because small numbers of squirrels were available for collaring on all treatments except the FOOD and PREDATOR EXCLOSURE+FOOD treatments, particularly in 1993 and 1994. Survival of radio-collared adults from different study sites was also combined to determine whether survival differed among years. Survival of radio-collared adults was significantly lower in 1992 and 1993 than in 1994 and 1995 (Table 2.2).

The PREDATOR EXCLOSURE and PREDATOR EXCLOSURE+FOOD treatments did not significantly or consistently increase survival of radio-collared juveniles in any year (Table 2.2; Figure 2.3). Statistical power to detect
differences among treatments and among years varied from 0.5 to 0.8. Juvenile survival was almost significantly lower in 1994, in contrast to 1993 and 1995 (Table 2.2).
FIGURE 2.3.

(a) 28-day survival (with 95% Confidence Limits) of radio-collared adult ground squirrels during the active season on four CONTROL grids, two FOOD addition treatments, a PREDATOR EXCLOSURE treatment, and a PREDATOR EXCLOSURE+FOOD treatment, 1992 - 1995.

(b) 28-day survival (95% C.L.) of radio-collared juvenile ground squirrels in their first active season on two CONTROL grids (A and D), a FOOD addition treatment (FOOD 1), a PREDATOR EXCLOSURE treatment, and a PREDATOR EXCLOSURE+FOOD treatment, 1993 - 1995.
**TABLE 2.2.** Results of statistical analyses (adapted for MS-DOS from Pollock *et al.* (1989) by C. J. Krebs, unpublished) to compare survival of radio-collared adult arctic ground squirrels (1992 to 1995) and juvenile arctic ground squirrels (1993 to 1995) among three experimental treatments and four controls, and to compare pooled survival on all treatments among years.

<table>
<thead>
<tr>
<th></th>
<th>$\chi^2$</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>3.65</td>
<td>3</td>
<td>0.30</td>
</tr>
<tr>
<td>1993</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>3.73</td>
<td>3</td>
<td>0.44</td>
</tr>
<tr>
<td>Juveniles</td>
<td>6.11</td>
<td>3</td>
<td>0.10</td>
</tr>
<tr>
<td>1994</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>4.93</td>
<td>3</td>
<td>0.29</td>
</tr>
<tr>
<td>Juveniles</td>
<td>6.25</td>
<td>3</td>
<td>0.10</td>
</tr>
<tr>
<td>1995</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>5.88</td>
<td>3</td>
<td>0.21</td>
</tr>
<tr>
<td>Juveniles</td>
<td>4.83</td>
<td>3</td>
<td>0.19</td>
</tr>
<tr>
<td>between-years</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>159.45</td>
<td>3</td>
<td>&lt;0.0001**</td>
</tr>
<tr>
<td>Juveniles</td>
<td>5.58</td>
<td>2</td>
<td>0.06*</td>
</tr>
</tbody>
</table>

** Adult survival was significantly lower in 1992 and 1993 than in 1994 and 1995.

* Juvenile survival was almost significantly lower in 1994 than in 1993 or 1995.
Rates of population change

On all experimental treatments and controls, instantaneous rates of population change were positive from 1990 to 1991, negative with one exception from 1991 to 1993, and positive with one exception from 1993 to 1995 (Figure 2.4). This trend was consistent on both control and treatment grids in most years. In contrast to all other treatments and controls, the PREDATOR EXCLOSURE+FOOD treatment sustained a positive rate of population growth from 1991 to 1992, and the population declined for only one year (1992 to 1993) on this treatment before increasing from 1993 to 1995 (Figure 2.4). Both juvenile and adult survival influenced rates of population change from 1993 to 1995 (juveniles: $r^2=0.74; F=17.23; n=8; p<0.006$; adults: $r^2=0.82, F=46.96; n=12; p<0.0001$; Figure 2.5). Influence of juvenile survival on population growth rates could be measured for only 1993 to 1995 because juveniles were radio-collared only from 1993 to 1995, when arctic ground squirrel populations were increasing.
FIGURE 2.4. Instantaneous rates of population change per year, $r$ (calculated as $r = \ln[N(t+1)/N(t)]$) on four CONTROL grids, two FOOD addition treatments, a PREDATOR EXCLOSURE treatment, and a PREDATOR EXCLOSURE+FOOD treatment from spring 1990 to spring 1995.
1.5 - 1.5

\[ r \]


Spring of year t+1

Instantaneous rate of population change, r

Controls

P.Ex.

Foods

P.Ex.+Food

45
FIGURE 2.5.

(a) \( R \) (finite rate of increase or \( N(t+1)/N(t) \) ratio) as a function of adult survival, from spring 1992 to spring 1995. Each point represents a spring:spring ratio on a particular experimental treatment or on controls (CONTROLS A - D pooled and FOODS 1 & 2 pooled).

(b) \( R \) as a function of juvenile survival from spring to spring 1993 to 1995. Each point represents a spring:spring ratio on a particular experimental treatment or control. Juvenile survival was measured in active seasons 1993 to 1995 only, so no data on juvenile survival were available prior to 1993 when \( R \) was <1.
Juveniles $r^2=0.74; \ p<0.006; \ F=17.23; \ n=8$

Active season survival

(a)

(b)

Adults $r^2=0.82; \ p<0.0001; \ F=46.96; \ n=12$

Finite rate of increase, $R$ (spring $N(t+1)/N(t)$)
Concurrent changes in other species in the boreal forest community

Snowshoe hare biomass declined from 1989 to 1993 (Figure 2.6a). Biomass of mammalian and avian predators peaked in 1990 and 1992, respectively (Figures 2.6b and 2.6c). Arctic ground squirrel biomass peaked in the boreal forest in 1991 and was lowest in 1993 (Figure 2.6d), whereas adult arctic ground squirrel survival declined from 1990 to 1993 (Figure 2.6e).
FIGURE 2.6.

(a) Biomass (kg/ha) of snowshoe hares on control areas, 1989 - 1995. Methods for estimating snowshoe hare density and biomass are described in the text. Data were used with permission from C. J. Krebs (pers. comm.).

(b) Biomass (kg/350km$^2$) of mammalian predators (lynx and coyotes), 1989 - 1995. Methods for estimating mammalian predator densities and biomass are described in the text. Data were used with permission from M. O’Donoghue (thesis submitted).

(c) Biomass (kg/100km$^2$) of avian predators (great horned owls, red-tailed hawks, and goshawks), 1989 to 1995. Methods for estimating avian predator densities and biomass are described in the text. Data were used with permission from F. Doyle (pers. comm.).

(d) Biomass (kg/ha) of arctic ground squirrels on control areas, 1990 to 1995. Biomass was calculated by multiplying the average weight of an adult ground squirrel (0.4 kg) by population density in spring on CONTROLS A-D pooled.

(e) 28-day active season survival of adult arctic ground squirrels on control sites, 1990 to 1995, and 28-day survival of juvenile arctic ground squirrels on control sites, 1993 to 1995. Active season survival in 1990 and 1991 was estimated from trapping data and in 1992 from radio telemetry by Hubbs and Boonstra (in press).
Discussion

I have presented experimental evidence that both predation and food supply limit arctic ground squirrel population densities, and that they interact to limit arctic ground squirrel populations in the northwestern boreal forest regions of North America during the decline and low phases of the snowshoe hare cycle. Whereas predator removal doubled arctic ground squirrel populations, on average, and food addition quadrupled population densities, simultaneous removal of predators and addition of food increased population densities 10-fold. These findings support the hypothesis that an interaction exists between predation and food supply in limiting arctic ground squirrel populations at Kluane (Hypothesis 3).

Food addition increased adult and juvenile growth rates, body condition, and reproduction in arctic ground squirrels at Kluane (Karels 1996), and the interactive effects of food and predation were best observed when considering growth and reproduction in arctic ground squirrel populations. However, body condition of adult females, litter sizes, percentage of females producing a litter to emergence, and growth rates of juvenile females were not significantly higher on the PREDATOR EXCLOSURE treatment compared with CONTROLS from 1993 to 1994 (Karels 1996), which suggests that an interaction between predation and
food supply was manifest through a combination of reproductive and survival parameters on the FOOD and PREDATOR EXCLOSURE+FOOD treatments. In addition, Baker (1996), working on my study sites, found no differences between controls and the experimental treatments in the amount of time spent foraging or vigilant. In my study, food and predation did not interact to affect adult survival, juvenile survival, or population growth rates. However, adult survival was generally (but not significantly) higher on the experimental treatments than on the controls (Figure 2.3), and probably interacted with the reproductive parameters described by Karels (1996) to produce the more than 10-fold increase in population density on the PREDATOR EXCLOSURE+FOOD treatment.

Results of food-supplementation experiments on small mammal species generally show decreases in home range size (Mares et al. 1982) and increases in population density, immigration of non-residents to food-supplemented areas, and recruitment of juveniles into the population (Gilbert and Krebs 1981; Taitt and Krebs 1981; Dobson and Kjelgaard 1985a,b; Boutin 1990; Klenner and Krebs 1991; Dobson 1995). Arctic ground squirrels in the boreal forest showed similar responses to food addition (decreased home range size: Appendix IV; reproductive parameters: Karels 1996). Similar interactions were observed by Desy and Batzli (1989) and Desy et al. (1990) when they examined the
simultaneous effects of food supply and predation on home range size, aggression, population density, growth rates, and body mass in field populations of prairie voles (*Microtus ochrogaster*).

Although the observed increases in adult survival on experimental treatments were not statistically significant, the influence of survival on arctic ground squirrel population trends from 1990 to 1995 was clearly demonstrated by the negative population growth rates and decline in adult active season survival from 1991 to 1993 when the ratio of predators to ground squirrels was high, and when predation intensity was probably highest. I used biomass of predators and snowshoe hares as an index to show that arctic ground squirrel populations had reduced survival and declines in population densities and growth rates, possibly as a result of the snowshoe hare cyclic decline. Active season survival of adult arctic ground squirrels was lowest in 1992 and 1993, when predators were using arctic ground squirrels as alternative prey during summer (Rohner 1994; M. O’Donoghue, pers. comm.; F. Doyle, pers. comm.). In addition, adult survival was consistently high in 1994 and 1995, when predator biomass (and possibly predation intensity) was lowest, and adult and juvenile survival had a strong effect on population growth rates from 1992 to 1995. During my study, overwinter losses of radio-collared squirrels were small (Appendix II) although Hubbs and
Boonstra (in press) suggested that high overwinter loss in the 1991 to 1992 winter contributed to the decline in arctic ground squirrel populations immediately following the snowshoe hare decline. However, the changes in active season survival from 1992 to 1995 suggest that active season survival was also important in influencing arctic ground squirrel population trends in the boreal forest during this time.

Other studies have demonstrated increased survival of prey species following predator removal. Newsome et al. (1989) observed a four-fold increase in rabbit numbers over three years in Australia after rabbit predators were experimentally removed. Similar declines in populations of “alternative prey” have been observed elsewhere. Keith and Cary (1991) observed that increased predation occurred on populations of alternative prey (including Franklin’s ground squirrels, *S. franklinii*) during a snowshoe hare population decline in Alberta. Steenhof and Kochert (1988) reported that Townsend’s ground squirrels (*S. townsendii*) were alternative prey for golden eagles (*Aquila chrysaetos*) during a jackrabbit (*Lepus californicus*) decline in Idaho. Marcstrom et al. (1989) concluded that arctic hare (*Lepus timidus*) population densities and growth rates declined in response to increased predation by red foxes (*Vulpes vulpes*) and martens (*Martes martes*) when *Microtus* and *Clethrionomys* populations declined.
on two islands in the northern Baltic sea. Sutherland (1988) summarised evidence that changes in survival rates of Brant geese may be due to predators such as arctic foxes (*Alopex lagopus*) switching to goose eggs and goslings as a consequence of the cyclic decline of lemmings on the Taimyr peninsula in Siberia. In the boreal forests of North America, some species of small herbivores (red squirrels, *Microtus*, and *Clethrionomys* spp.) do not fluctuate in synchrony with the snowshoe hare cycle (Boutin *et al.* 1995). Stuart-Smith and Boutin (1995) concluded that predation did not have a measurable impact on red squirrel population densities at Kluane, and that red squirrels did not show a secondary cycle as a result of the snowshoe hare cycle. Unlike red squirrels, arctic ground squirrel population densities were significantly correlated with snowshoe hare population densities (Boutin *et al.* 1995).

Although population densities and growth rates were influenced by the interaction between predation and food, juvenile survival was not. In particular, survival of juveniles was not significantly different among treatments. Juvenile mortality is related to dispersal distance (Chapter 3), and dispersing juveniles showed similar exploratory behaviour regardless of experimental treatment, so were probably susceptible to the same intensity of predation as juveniles from control areas. Predator exclusion was not entirely successful, because squirrels (both adults and
juveniles) were able to move freely in and out of the experimental treatments. Occasionally such movements resulted in a predation event, and squirrels that moved outside the relative safety of the fences and monofilament were as susceptible to predation as squirrels from control and food-supplemented sites. Juvenile survival did not differ among years during the low phase of the snowshoe hare cycle (1993 to 1995), and had less influence than adult survival on population growth rates during this time. Further work should focus on the impact of juvenile survival on overall population trends when predators are more abundant during the increase and peak phases of the snowshoe hare cycle.

Large-scale experimental manipulations are often costly to maintain and difficult to replicate (Carpenter et al. 1995; Krebs et al. 1995). Hence, the PREDATOR EXCLOSURE and the PREDATOR EXCLOSURE+FOOD treatments were not replicated in my study. Drawing conclusions from ecological studies without replication can be problematic (Hurlbert 1984). However, I believe that the observed changes in population density on the experimental treatments were real for the following reasons. Firstly, although the PREDATOR EXCLOSURE+FOOD and the PREDATOR EXCLOSURE treatments were unreplicated, control sites were replicated. Similar changes in population densities and survival of arctic ground squirrels were observed among all
controls. Secondly, all my study grids were located on areas of similar habitat (predominantly open spruce and shrub-meadow; Hubbs and Boonstra, in press). Hence, observed demographic changes are unlikely to be site-specific anomalies. Finally, strong responses to food-supplementation have been observed in other species of small mammals (Boutin 1990), including ground-dwelling sciurids (e.g., Dobson and Kjelgaard 1985a,b; Dobson 1995), so the high population densities on food-supplemented areas in my study were not unexpected.

In this paper I have provided evidence that both predation and food limit ground squirrel populations in the boreal forest. Arctic ground squirrel populations have demonstrated fluctuations in density and survival as a consequence of the snowshoe hare cyclic decline that suggest that the snowshoe hare cycle indirectly affects the arctic ground squirrel as an alternative prey. In Chapters 3 and 4 I explore the role of food and predation in juvenile survival, dispersal, and philopatry in arctic ground squirrel populations in the boreal forest.
Summary

In a large-scale experiment, I tested the effects of predation and food on an arctic ground squirrel population during the decline and low phases of a snowshoe hare cycle. From 1990 - 1995, populations were monitored in northern boreal forest at Kluane, Yukon Territory, Canada (61°N, 138°W). Squirrels were studied on eight 9-ha grids: four unmanipulated CONTROL grids, two FOOD-supplemented grids, a PREDATOR EXCLOSURE grid lacking terrestrial mammalian predators, and a PREDATOR EXCLOSURE+FOOD grid.

I measured population density on all areas using live-trapping and survival of adults and juveniles using radio-telemetry. Population densities and adult survival rates were lowest on all treatments in 1992 and 1993 (two years after the snowshoe hare population decline) but were high in all other years. Population growth rates were negative from 1991 to 1993 when predation pressure was most intense, and positive from 1993 to 1995 following a decline in predator densities. Juvenile survival from 1993 to 1995 was on average 25% lower than adult survival and was unaffected by changes in predation intensity.
On average, predator exclusion doubled population densities, food-supplementation quadrupled population densities, and food-supplementation and predator removal together resulted in a 10-fold increase in arctic ground squirrel population densities. Food and predation interact to limit arctic ground squirrel populations in the boreal forest during the decline and low phases of the snowshoe hare cycle. I conclude that the increase in predator numbers as a result of the cyclic fluctuation in snowshoe hare densities creates a secondary fluctuation in arctic ground squirrel population densities and survival.
Literature cited


Hubbs, A. H. 1994. The effects of food and predation on population regulation of the arctic ground squirrel (Spermophilus parryii plesius) during the peak and decline phases of a snowshoe hare cycle. M.Sc. Thesis, University of Toronto, Canada.


CHAPTER 3: NATAL DISPERSAL OF JUVENILE ARCTIC GROUND SQUIRRELS IN THE BOREAL FOREST

Introduction

Natal dispersal is defined as the movement of pre-reproductive individuals from their place of birth to a new home range where they may attempt to breed (Howard 1960; Greenwood 1980; Stenseth and Lidicker 1992). It is a subject of intense interest to ecologists because it has been linked to a wide range of demographic and life history traits (Arcese 1989; Stenseth and Lidicker 1992). The costs and benefits of dispersal may differ among age and sex classes in a population, depending on a number of ecological and environmental factors such as mating systems and social behaviour (Greenwood 1980, 1983; Waser and Jones 1983; Wolfenden and Fitzpatrick 1984), optimal inbreeding (Shields 1982, Waser et al. 1986), habitat heterogeneity (Cockburn 1992; Gliwicz 1992), mate competition (Dobson 1982; Moore and Ali 1984), and population cycles (Lidicker 1975; Krebs 1992, 1996).

To understand the ecological consequences of natal dispersal, we need to know the fate of dispersing individuals. Recent reviews of dispersal (e.g., Greenwood
and Harvey 1982; Shields 1987; Gaines and Johnson 1987; Anderson 1989; Stenseth and Lidicker 1992), and field studies (e.g., Greenwood et al. 1979; Garrett and Franklin 1988; Arcese 1989; Wiggett and Boag 1989; Larsen and Boutin 1994; Van Vuren and Armitage 1994) have all emphasised the need to follow individual dispersers if we are to gain a greater understanding of the causes and consequences of natal dispersal.

Natal dispersal is common among ground-dwelling sciurids and is usually sex-biased toward males (Michener and Michener 1977; Sherman 1977; Michener 1981, 1983; Holekamp 1984a, 1986; Wiggett et al. 1989). Dispersal is often associated with high mortality (Gaines and McClenaghan 1980; Michener 1983; Stenseth 1983). Poor survival of juvenile males during dispersal may contribute to the female-biased adult sex ratio in ground-dwelling sciurids (Michener and Michener 1977; Schmutz et al. 1979; Wiggett and Boag 1992). Yet the fate of dispersing individuals is not often studied because of the inherent difficulties in identifying and tracking dispersers (Holekamp 1984b, McShea and Madison 1992, Waser et al. 1994). McShea and Madison (1992) highlighted some advantages of using radio-telemetry to identify dispersing individuals and to determine their fate, and this technique has been used to successfully estimate sex bias, movement patterns, and survival of dispersers (e.g., Hackett 1987; Wiggett et al. 1989;
Ultimate (evolutionary) causes of animal dispersal have received much attention in the literature (Bengtsson 1978; Greenwood 1980, 1983; Dobson 1982; Waser 1985; Waser et al. 1986; Holekamp 1986; Shields 1987; Lidicker and Stenseth 1992). It has been proposed that individuals disperse to avoid competition for mates (Dobson 1982; Moore and Ali 1984) or to avoid inbreeding (Cockburn et al. 1985; Packer 1985; Waser et al. 1986; Halpin 1987). Food resource limitation is also sometimes regarded as an ultimate cause of dispersal in mammals (Dobson and Jones 1985; Halpin 1987; Lidicker and Stenseth 1992).

My objective was to investigate the consequences of dispersal and philopatry for individual juvenile arctic ground squirrels (*Spermophilus parryii plesius*). My first hypothesis addresses the survival cost of dispersal, whereas my second hypothesis attempts to distinguish among three explanations for natal dispersal. I define **emigration** as the movement of a juvenile away from its natal area. Emigration may result in **dispersal** if the individual moves more than one average adult female home range diameter from its natal area and remains in the new location to breed (Howard 1960; Greenwood 1980). Conversely, I consider
philopatry to be minimal emigration resulting in a juvenile reaching reproductive age within one average adult female home range from the natal burrow or within contact of the maternal home range (Anderson 1989; Greenwood 1980; Waser 1988).

**Hypothesis 1:**

**Dispersing juvenile arctic ground squirrels are at higher risk of mortality than philopatric individuals.**

In this hypothesis I focus on the survival consequences of dispersal and provide an estimate of survival during dispersal on four experimental treatments. Three predictions arise from this hypothesis:

(1) Squirrels that move longer distances from their birthplace will have a greater chance of pre-winter mortality;

(2) If mortality during dispersal is due to predation, then juveniles protected from predators will have higher survival than control juveniles; and

(3) Males will have higher mortality rates than females (in this species, males are usually the dispersing sex; Carl 1971; Green 1977; Lacey 1991).
Hypothesis 2:

Three hypotheses have been proposed to explain natal dispersal in the context of mating systems: the competition for mates (CFM) hypothesis; the competition for resources (CFR) hypothesis; and the inbreeding avoidance (IA) hypothesis (Dobson 1982; Dobson and Jones 1985). In attempting to distinguish between these three alternatives, I consider males and females separately.

Hypothesis 2a: Juvenile arctic ground squirrels disperse in response to a shortage of limiting resources such as food (CFR hypothesis).

Similar predictions can be made for males and females:

(1) Dispersal distances will be shorter on food-supplemented areas;
(2) Proportionally fewer juveniles will disperse from food-supplemented areas;
(3) The proportion of individuals dispersing will increase with increasing population density if food is limiting at high density; and
(4) The proportion of juveniles dispersing will approximately equal adult annual survival, if juveniles are merely replacing resident adults that die.

Hypothesis 2b: Juvenile males disperse in response to intrasexual competition for mates (CFM hypothesis).

Because of the polygynous mating system in arctic ground squirrels (Carl 1971; Lacey 1991), it is unlikely that juvenile females disperse to avoid competition for mates (Dobson 1982), so the following predictions apply only to males:
(1) The proportion of juvenile males dispersing will be no greater than annual survival of adult males; and

(2) Food-supplementation will not affect juvenile male dispersal distances or the proportion of males dispersing.

**Hypothesis 2c: Juveniles disperse to avoid inbreeding with close relatives (IA hypothesis).**

Predictions:

(1) Juveniles will disperse independently of the adult same-sex disappearance rate;

(2) Juveniles of both sexes will disperse at least one opposite-sex adult home range diameter from their natal site to avoid inbreeding with opposite-sex kin;

(3) Food-supplementation will not affect dispersal distances or dispersal frequency of either sex.
Methods

Study sites
Dispersal movements and survival of juvenile arctic ground squirrels were studied on five 9-ha experimental grids containing 100 grid points spaced 30 m apart in a 10x10 array: (1) two unmanipulated CONTROL grids (CONTROLS A and D); (2) a FOOD grid provisioned ad lib with pelleted rabbit chow (minimum 16% crude protein) distributed by fertiliser spreader along four 600 m cut lines ("feeder rows"); (3) a PREDATOR EXCLOSURE grid which was a 1-km² area surrounded by an 8600-Volt electric fence to deter large terrestrial predators and partially covered by monofilament lines spaced approximately 30 cm apart in an attempt to deter avian predators; and (4) a PREDATOR EXCLOSURE + FOOD grid which was a 1-km² area surrounded by an electric fence and provisioned with pelleted rabbit chow, as described above.

Field methods
Natal dispersal and survival of juveniles were monitored in 1993, 1994, and 1995. Juveniles emerged from the natal burrow in mid to late June each year (emergence dates are shown in Appendix V). All juveniles were trapped in Tomahawk live traps, tagged with Monel No. 1005-1 tags (National Band and
Tag Co.) in both ears, weighed to the nearest 2 g using a Pesola spring scale, sexed, and radio-collared with expandable collars (for a description of the radio collars, see Appendix I). Radios were SM-1 transmitters (AVM, California) with Hg-675 batteries, and SS-2 transmitters (Biotrack, England) with Hg-675 batteries. Range of the radio-transmitters varied from 300 m to 500 m, depending on topography, shrub cover, and whether individual squirrels were above or below ground.

I collared at least two juveniles (one male and one female) per litter for a total of 8 - 18 juveniles per treatment in each year. A total of 195 juvenile arctic ground squirrels were radio-collared (59 in 1993, 66 in 1994, and 70 in 1995). Of these, 23 were not used for analysis because their radio-collars fell off immediately or were chewed off by the mother (22 individuals) or because they were killed on the Alaska highway (one individual). Fates of the 195 juveniles collared are shown in Figure 3.1. I located each individual once every two days with a hand-held antenna.
FIGURE 3.1: Fates of 195 juvenile arctic ground squirrels radio-collared at emergence from the natal burrow on two control and three experimental treatments, 1993 to 1995.
195 juveniles collared

23 eliminated from analysis

172 potential dispersers

22 juveniles lost

150 followed to hibernation or death

90 survived to hibernation

60 mortalities
I measured the emigration distance of each juvenile as the straight-line distance between its place of birth (natal burrow or mother's home burrow) and its sleeping burrow in autumn prior to hibernation. I focussed on sleeping burrow locations because they provided precise end points (after Hackett 1987). Sleeping burrows were located by radio-tracking sleeping individuals before sunrise (=0700h) in late August. On-grid dispersal distance was calculated using the grid co-ordinate system. Dispersal distances of juveniles that moved beyond the study sites were determined with a Trimble Basic GPS (global positioning system). GPS co-ordinates obtained in the field were accurate to within approximately 20 m after being differentially corrected using a base station at the Kluane Lake Research Station.

I made three assumptions in this study. All juveniles (males and females) were classified as "dispersers" if they moved farther than one average adult female home range diameter from the natal burrow (Howard 1960; Greenwood 1980). Consequently individuals had to have moved different distances from their birthplace on different grid treatments because female home ranges were smaller on treatments supplemented with food (Appendix IV). I also assumed that for every depredated individual, the point of death (where the radio was found) was that squirrel's emigration or dispersal distance. Some squirrels would doubtless
have dispersed farther had they survived, but there was no way of knowing where these individuals would have stopped. Finally, 22 juveniles (two females and 20 males) were lost during my study. Usually, the radio signal could no longer be picked up, and extensive searches were carried out on the treatment areas and for a radius of at least 1000 m around each area. Although I had no estimate of survival for any of these individuals, their dispersal distances were assumed to be a conservative 500 m. Some radio-collars may have failed; however, no squirrels with non-functional collars were caught during extensive trapping sessions on the study sites in autumn each year. I assumed that all 22 of these lost individuals dispersed beyond the study areas.

**Statistical analyses**

All statistical analyses were carried out using JMP for Macintosh (SAS Institute 1994). Data were tested for normality and homoscedasticity, and were log-transformed where appropriate. Nonparametric tests were carried out if the data did not satisfy these assumptions after transformation. I used a log-linear analysis to determine the effects of sex (male or female), treatment (CONTROLS, PREDATOR EXCLOSURE, FOOD, and PREDATOR EXCLOSURE+FOOD), dispersal (dispersed or philopatric) and year (1993, 1994, or 1995) on juvenile survival. I used logistic regression to compare
emigration distances of male and female squirrels, with distance as the continuous variable and the two sexes as a binomial dependent variable. Contingency table analyses were performed to compare the proportion of individuals dispersing among treatments and controls and to compare the proportion of males and females killed. I used G-tests (Sokal and Rohlf 1995) to determine whether each sex was more or less likely to disperse than expected on the basis of adult annual survival. Estimates of juvenile survival on each treatment were compared using formulas in Pollock et al. (1989) and modified for use with MS-DOS by C. J. Krebs (Unpublished) as described in Chapter 2.
Results

Population trends and survival 1993 to 1995

In Chapter 2 I showed that population densities of arctic ground squirrels on PREDATOR EXCLOSURE, FOOD, and PREDATOR EXCLOSURE+FOOD treatments were two to 10 times higher than those on controls (Figures 2.1 and 2.2). Densities on the PREDATOR EXCLOSURE+FOOD treatment in 1995 were particularly high (45.6 squirrels/ha in summer 1995). I also found no significant difference in juvenile survival among treatments and controls in any year (Figure 2.3). Juvenile squirrels from the PREDATOR EXCLOSURE and PREDATOR EXCLOSURE+FOOD treatments did not survive significantly better than squirrels from other study sites, often because they dispersed beyond the relative safety of the fences or monofilament and were therefore susceptible to the same predation intensity as squirrels from FOOD and CONTROL areas. Juveniles from the PREDATOR EXCLOSURE+FOOD treatment in 1995 had the highest mortality rates (Figure 2.3).

Sex-specific dispersal

Distances dispersed by juvenile females were strongly biased toward zero whereas those of juvenile males were less so (Figure 3.2). Overall, juvenile
females moved a mean (± S.E.) of 120.3 ± 27.9 m, and a median of 60.0 m from their natal area. Juvenile males moved a mean of 515.0 ± 106.6 m, and a median of 240.5 m from their natal area (Figure 3.2). For juvenile males, median and mean dispersal distances are probably underestimates because I lost 20 males, many of which were likely to have been long-distance dispersers. Over half (68%) of all juveniles classified as dispersers were male, and males dispersed significantly longer distances than females (logistic regression: n=172; $r^2=0.16$; df=1; $p<0.0001$) when all treatments and all years were combined (for a breakdown of sex bias in dispersal distance by treatment and year, see Appendix VI).

From live-trapping data, I calculated annual mortality of adult females to be 0.47. Hence, if juvenile females were claiming spaces that became available, 47% would be expected to stay and 53% would be expected to disperse. However, most (88%) females were philopatric and females were significantly more likely to remain philopatric than expected ($G=25.76; \chi^2=10.83; df=1; p<0.001$). Similarly, I calculated adult male annual mortality to be 0.78. If juvenile males were filling available spaces left vacant by adult males, 78% of juvenile males would be expected to remain philopatric and 22% would be expected to disperse. Yet only 28% of juvenile males were philopatric and 72%
Males were significantly more likely to disperse than expected on the basis of annual mortality or disappearance of adult males (G=55.8; χ²=10.83; df=1; p<0.001).

Mean emigration distances varied both within and among experimental treatments, but not in any consistent pattern (Figure 3.3). Male dispersal distances did not differ among years (Kruskal-Wallis test: χ²=0.04; df=2; n=70; p>0.98) whereas females had significantly longer dispersal distances in 1995 than in 1993 or 1994 (Kruskal-Wallis test: χ²=9.23; df=2; n=102; p<0.01), probably because females on the PREDATOR EXCLUSION+FOOD treatment dispersed unusually long distances in 1995 (more than 10 times as far as on other treatments in other years; Figure 3.3). Broken down by treatment and by year, there were no differences among treatments in male or female dispersal distances (Appendix VII) except for the PREDATOR EXCLUSION+FOOD treatment in 1995. When all three years were combined, there were no significant differences among grid treatments in juvenile male and female dispersal distances (Kruskal-Wallis test; females: χ²=2.33; df=3; p>0.50; n=102; males: χ²=1.11; df=3; p>0.77; n=70). Neither sex dispersed shorter distances on treatments with supplemental food in any year.
FIGURE 3.2. Frequency distribution of dispersal distances of 50 radio-collared juvenile males and 100 juvenile females. Juveniles from all treatments and all years are combined in this graph. Arrows show the median dispersal distances of females (F; 60.0 m) and males (M; 240.5 m). Two females and 20 males that were not located (so might have dispersed) are not included in this graph. For males in particular, this biases the median towards zero.
FIGURE 3.3. Mean (± S.E.) distance from birthplace to point of death or to core area of a new home range, for male and female juvenile arctic ground squirrels on two control areas and three experimental treatments, 1993 to 1995. The first column of each pair represents males and the second column represents females. Sample sizes are shown above each bar. Asterisks above juveniles from the PREDATOR EXCLOSURE+FOOD treatment in 1995 indicate that dispersal distances of juveniles from this treatment were significantly longer than any other juveniles on any other treatment in any other year.
Dispersal and survival

Juvenile squirrels that died moved a mean (± S.E.) of 512.1 ± 125.5 m (median 143.5 m) from their natal area whereas squirrels that survived their first active season moved a mean of 143.8 ± 24.6 m (median 61.5 m). Most (97%) juvenile squirrels died from predation (see Appendix III for a summary of proximate causes of mortality). In addition, a higher proportion of individuals classified as dispersers died in all years (Figure 3.4). Overall, 27 of 51 dispersers (53%) died, whereas 18% (18 of 99) non-dispersers died (G=32.34; df=1; \(\chi^2=10.83\); p<0.001). This trend was clear on the three treatments, but reversed on control areas, and was consistent among years.

Log-linear analysis of the effects of sex, treatment, year, and dispersal on juvenile survival revealed a significant interaction between dispersal and survival (juveniles that moved longer distances from their natal burrows were more likely to die; \(\chi^2=116.35\), df=92; p<0.04). Males were significantly more likely to die than females, and there was also an interaction between sex and survival that was almost significant (\(\chi^2=114.43\), df=92; p<0.06). Whereas more juvenile males were classified as dispersers, and males were more likely to die, some juvenile females also dispersed long distances and died. Although mortality was usually male-biased, it was female-biased on the PREDATOR EXCLOSURE+FOOD
treatment in 1995. Survival of juveniles from each treatment in each year was negatively related to dispersal distance (Figure 3.5; $r^2=0.53$; n=24; F=25.22; p<0.0001). For a breakdown of survival as a function of dispersal distance by treatment and year, see Appendix VIII.
FIGURE 3.4. Proportion of dispersing and philopatric juvenile arctic ground squirrels that died on all treatments and controls, 1993 to 1995. P.EX. = PREDATOR EXCLOSURE. Sample sizes are shown above each bar.
FIGURE 3.5. Survival of juvenile male and female arctic ground squirrels as a function of average dispersal distance on each grid. Each point represents 3-13 radio-collared squirrels on a particular treatment in a particular year (n=12 treatment-years).
Survival from emergence to hibernation vs. mean distance from natal burrow (m).

- Females: ○
- Males: ★

The graph shows a negative correlation between survival and distance from the natal burrow, with females generally surviving longer at shorter distances than males.
Proportion of individuals dispersing from treatments

From 1993 through 1995, between 21% and 87% of radio-collared juveniles dispersed from the grid treatments (Table 3.1). The proportion of dispersers was constant among treatments in each year, with the exception of the PREDATOR EXCLOSURE+FOOD treatment in 1995, which had a significantly higher proportion of dispersers (Table 3.1). Plotting the rate of dispersal of both sexes from the experimental treatments as a function of density of adults in spring (Figure 3.6) revealed only weak density dependence in dispersal tendency (males: \( r^2 = 0.06; n=12; F=0.73; p>0.41 \); females: \( r^2 = 0.51; n=12; F=10.20; p<0.01 \); females with PREDATOR EXCLOSURE+FOOD treatment in 1995 removed: \( r^2 = 0.03; F=0.29; p>0.60, n=11 \)). At artificially high densities (on the PREDATOR EXCLOSURE+FOOD treatment in 1995), density dependence in dispersal tendency was stronger for females, but not for males (Figure 3.6).
TABLE 3.1. Proportion of juvenile arctic ground squirrels of both sexes classified annually as dispersers (moved more than one adult female home range diameter) on all treatments. Significantly more juveniles dispersed from the PREDATOR EXCLOSURE+FOOD treatment than on other sites in 1995.

<table>
<thead>
<tr>
<th>TREATMENT</th>
<th>n</th>
<th>Proportion dispersing</th>
<th>$\chi^2$</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993 Controls</td>
<td>8</td>
<td>0.50</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>P.Ex.</td>
<td>17</td>
<td>0.53</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Food</td>
<td>15</td>
<td>0.67</td>
<td>1.34</td>
<td>3</td>
<td>0.72</td>
</tr>
<tr>
<td>P.Ex.+Food</td>
<td>11</td>
<td>0.45</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1994 Controls</td>
<td>12</td>
<td>0.25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.Ex.</td>
<td>15</td>
<td>0.27</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Food</td>
<td>18</td>
<td>0.22</td>
<td>2.73</td>
<td>3</td>
<td>0.44</td>
</tr>
<tr>
<td>P.Ex.+Food</td>
<td>15</td>
<td>0.47</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1995 Controls</td>
<td>16</td>
<td>0.25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>P.Ex.</td>
<td>14</td>
<td>0.21</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Food</td>
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<td>0.33</td>
<td>16.82</td>
<td>3</td>
<td>&lt;0.001</td>
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<tr>
<td>P.Ex.+Food</td>
<td>15</td>
<td>0.87</td>
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</tr>
</tbody>
</table>
FIGURE 3.6. Proportion of juvenile male and female arctic ground squirrels dispersing as a function of density of adults in spring, 1993 to 1995. Each point represents 3-13 radio-collared individuals on a particular treatment in a particular year (n=12 treatment-years).
Population density in spring (adult squirrels/ha)

- **Males**
  - Proportion dispersing: 0.75
  - Proportion dispersing: 0.5
  - Proportion dispersing: 0.25
  - Proportion dispersing: 0

- **Females**
  - Proportion dispersing: 0.75
  - Proportion dispersing: 0.5
  - Proportion dispersing: 0.25
  - Proportion dispersing: 0

- Females: $r^2 = 0.03$
- Males: $r^2 = 0.06$
- Females: $r^2 = 0.51$
Discussion

Patterns of mortality and dispersal

In this paper I describe the fates of 172 juvenile arctic ground squirrels from emergence to hibernation. I did not reject the null hypothesis of no cost to dispersal for juvenile arctic ground squirrels. Juveniles that moved longer distances from their natal area were more likely to die, and males moved longer distances and had higher mortality than females. There was also a strong negative relationship between mean dispersal distance and survival on each treatment. It is often assumed that dispersal is risky because dispersers may be more susceptible to predators while in transit (e.g., Metzgar 1967; Schmutz et al. 1979; Gaines and McClenaghan 1980; Greenwood and Harvey 1982; Stenseth 1983; Waser et al. 1994). My study verifies these assumptions for a polygynous ground-dwelling sciurid.

Evidence for higher mortality of dispersing individuals is mixed. In some studies, dispersers are known or suspected to have lower survival than philopatric individuals. Schmutz et al. (1979) concluded that disappearance of juvenile Richardson's ground squirrels (S. richardsonii) during dispersal was probably due to predation mortality. Wiggett et al. (1989) followed eight radio-collared
dispersers from a Columbian ground squirrel (*S. columbianus*) colony and estimated a minimum survival rate of 67% during dispersal, but they gave no estimate of survival for non-dispersing squirrels. Van Vuren and Armitage (1994) radio-tracked 123 yearling yellow-bellied marmots (*Marmota flaviventris*) over an 8-year period; survival of dispersers (73%) was lower than that of philopatric individuals (87%), but they concluded that survival was high enough to make dispersal a viable option. Garrett and Franklin (1988) estimated a 44% survival rate of inter-colony natal dispersers from a black-tailed prairie dog (*Cynomys ludovicianus*) colony, compared with a 90% survival rate for residents and non-dispersers.

In other studies, reported survival costs of dispersal are negligible. Hackett (1987) found no evidence that yearling Columbian ground squirrels were more likely to die while making excursions or while dispersing, and he concluded that dispersal was not more risky than philopatry. In his study, yearlings dispersed shorter distances than in my study (maximum 980 m, compared with 3815 m), and remained within a familiar open meadow habitat. Boyce and Boyce (1988) found the survival cost of dispersal in the field vole *Microtus arvalis* to be negligible (of 42 radio-collared juveniles, one young female disappeared (≈2%)). Greenwood *et al.* (1979) concluded that there was no mortality cost to natal
dispersal in great tits (*Parus major*). Holekamp (1984a) and Hackett (1987) both suggested that exploratory movements in Belding's and Columbian ground squirrels, respectively, serve to familiarise individuals with areas into which they may subsequently immigrate. If, as in my study, juveniles (particularly males) fail to remain within their area of initial exploration, they may be exposing themselves to greater risk of predation during dispersal. Likewise, squirrels from areas protected from predators did not have higher survival than control juveniles, because they often dispersed beyond the relative safety of the fences or monofilament.

On all treatment grids and in all years, juvenile male arctic ground squirrels consistently had higher mortality rates than females. This may explain the biased sex ratio among adults in arctic ground squirrels and is consistent with other ground-dwelling sciurids (e.g., Waterman 1992; Wiggett and Boag 1992). Michener and Michener (1977) suggested that yearling male Richardson's ground squirrels had higher mortality due to lower overwinter survival and possibly predation in their first year of life. Schmutz *et al.* (1979) observed that predation mortality fell disproportionately on male Richardson's ground squirrels, but found no disproportionate loss of males over winter. My study provides support for the idea that active-season survival before an individual
reaches reproductive age is probably a critical stage in the annual cycle of ground-dwelling sciurids (Michener and Michener 1977; Michener 1983).

The observation that male arctic ground squirrels moved, on average, farther than females is consistent with observations by Carl (1971), Green (1977), Schmutz et al. (1979), Holekamp (1984a,b), and Garrett and Franklin (1988) that young male sciurids disperse farther than females, although dispersing yearling and adult female Columbian ground squirrels have been reported to move at least as far as adult males (Boag and Murie 1981; Hackett 1987). In my study, males were more likely to make long-distance movements, although females also made large movements, the longest (1820 m) being from the PREDATOR EXCLOSURE+FOOD treatment in 1995. The high frequency of long-distance movements in males meant that I lost track of more males than females. Although I made no assumptions about the survival of these squirrels, it is likely that they died from predation in their first active season. If so, this strengthens the conclusion that differential mortality occurs during dispersal in this species. Likewise, estimates of mean and median dispersal distances for males were probably underestimates due to the greater likelihood of locating squirrels with shorter dispersal distances, so the differences I observed between male and
female dispersal distances, and between squirrels that died and squirrels that survived their first active season, were probably conservative.

**Hypotheses to explain the evolution of juvenile dispersal**

I observed little relationship between population density and dispersal rate in arctic ground squirrels. Juveniles from food-supplemented treatments did not have significantly shorter dispersal distances than control juveniles in any year, and food-supplemented populations had at least as many dispersers as the control populations in all years. Karels (1996) and Hubbs and Boonstra (in press) found that supplemental food increased juvenile birth weights, litter sizes, and adult body weights compared with control populations. Consequently, food-supplemented treatments at Kluane also had higher densities of ground squirrels. This may explain why a high proportion of juvenile females dispersed from the PREDATOR EXCLOSURE+FOOD treatment in 1995; despite the fact that supplemental food was being added to this treatment, natural food (herbaceous plants and willow leaves) was severely depleted (pers. obs.) and may have been limiting. Suitable burrow sites may also have been limiting. In addition, it is possible that arctic ground squirrels derive water from the food they eat, particularly in late summer (McLean 1985), so the PREDATOR EXCLOSURE+FOOD population in 1995 may have been water-limited. In
Chapter 2 I showed that arctic ground squirrel populations at Kluane were low and increasing from 1992 to 1995, so food resources and burrow sites may not have been limiting at this time. Future work on juvenile survival and dispersal should concentrate on clarifying the relationship between dispersal tendency of females and population density over the intermediate range of densities that I was unable to observe in this study.

Juvenile male arctic ground squirrels did not respond to supplemental food by decreasing their dispersal distances or tendency to disperse. Furthermore, more males dispersed from their natal area than expected on the basis of annual mortality of adult males. I can therefore reject the hypothesis that resource competition explains natal dispersal in juvenile male arctic ground squirrels. The inbreeding avoidance hypothesis is a better explanation for juvenile male dispersal in this species, although I cannot rule out the possibility that juvenile males also disperse to avoid intrasexual competition for mates. Conversely, juvenile females usually moved less than one adult female home range from their natal area, and remained philopatric more often than expected on the basis of adult female annual mortality. Juvenile female dispersal was high only at an unusually high population density, so the CFR hypothesis possibly explains juvenile female dispersal patterns in this species.
Dobson (1982) and Dobson and Jones (1985) have pointed out that the three hypotheses commonly proposed to explain the evolution of natal dispersal (competition for mates, competition for resources, and inbreeding avoidance) are not mutually exclusive. Consequently, juvenile males may be dispersing for the dual purpose of increasing access to unrelated mates and decreasing intrasexual competition (Dobson and Jones 1985). This is also a plausible explanation for the dispersal patterns I observed in male arctic ground squirrels. In addition, the conclusion that juveniles disperse to avoid inbreeding may be combining a number of different mechanisms. For example, Holekamp (1984b) concluded that Belding’s ground squirrels were dispersing to optimise inbreeding (after Shields 1982) rather than to completely avoid inbreeding. Clearly, the inbreeding avoidance hypothesis requires further investigation at both an ecological and a genetic level.

Available data indicate that resource limitation does not cause dispersal in juvenile male sciurids (Holekamp 1986), although it may influence dispersal and philopatry in females. Dobson (1979) supplemented a California ground squirrel (S. beecheyi) population with food for three months to determine whether food availability influenced yearling dispersal. Yearlings were not
radio-collared, but movements away from the natal home range were monitored on peripheral trapping grids. Young males disappeared from their natal colonies regardless of food availability, whereas young females moved to the supplemental food treatment or commuted regularly to it to obtain food. Dobson (1979) concluded that young males disperse to avoid inbreeding whereas young females disperse only if density is high relative to food availability. Dunford (1977) found no effect of supplemental food on dispersal of either sex in a round-tailed ground squirrel (*S. tereticaudus*) population. Dobson and Kjelgaard (1985) observed that supplemental food increased immigration of Columbian ground squirrels, particularly females, onto a food-supplemented site. However, in all these studies, no attempt was made to follow dispersers from food-supplemented sites to determine their survival relative to control squirrels. In my study, dispersing juveniles from food-supplemented populations had no survival advantage over juveniles from control areas.

A recurring problem in studies of dispersal is the confusion between proximate and ultimate causes of natal dispersal. For example, Holekamp (1986) cautions that resource limitation can be regarded as either a proximate or an ultimate cue for natal dispersal. Reproductive success of dispersing individuals may be enhanced by improving access to food resources and breeding sites (Greenwood
1980). Yet the proximate mechanism by which animals leave their natal area may also be resource limitation (Holekamp 1984b; 1986). Further work could focus on whether and how individuals of a particular age or sex class use resource limitation as the cue for dispersal.

Wolfenden and Fitzpatrick (1984) argued that cooperative breeding in Florida scrub jays (*Aphelocoma coerulescens*) evolved in response to limited opportunities for successful natal dispersal. Michener (1983) linked the evolution of sociality in ground-dwelling sciurids to the advantages of female philopatry and range sharing as well as the advantages of male dispersal and territoriality. It would be fruitful to examine the fitness consequences of philopatry and dispersal to further clarify the ultimate reasons for this continuum of strategies. In the following chapter I focus on the reproductive consequences of philopatry and dispersal for juvenile female arctic ground squirrels.
Summary

Natal dispersal is assumed to be costly because of the risk of mortality, yet rarely are movement patterns and survival of dispersers observed directly. I determined the fates and dispersal distances of 172 juvenile arctic ground squirrels from 1993 - 1995 at Kluane, Yukon Territory, Canada (61°N, 138°W) to measure the survival costs of dispersal. Juveniles were radio-collared at emergence from the natal burrow on two CONTROL areas, a PREDATOR EXCLOSURE treatment, a FOOD-supplemented treatment, and a PREDATOR EXCLOSURE+FOOD treatment in each year. I tested the hypothesis that dispersal has a high mortality cost.

In all years and on all treatments, juveniles that moved longer distances from their birthplace were more likely to die. Males dispersed farther than females and were more likely to die. I also attempted to distinguish among three hypotheses to explain natal dispersal: competition for mates, competition for resources, and inbreeding avoidance. Juvenile females were significantly more likely to remain philopatric than expected on the basis of adult female annual mortality, except on one treatment with high population densities where resources were possibly limiting. Resource competition possibly explains patterns of juvenile female dispersal and philopatry in arctic ground squirrels.
Juvenile males were significantly more likely to disperse than expected on the basis of annual disappearance of adult males from the population, and the proportion of males dispersing was unaffected by food availability, which suggests that males may ultimately disperse to avoid inbreeding with female relatives. The mortality costs of dispersal and philopatry, and the relative benefits of each, result in different dispersal characteristics in male and female arctic ground squirrels.
Literature cited


CHAPTER 4: FITNESS OF PHILOPATRIC AND DISPERSING FEMALE ARCTIC GROUND SQUIRRELS

Introduction

The fitness consequences of natal dispersal and philopatry are often debated because the costs and benefits to dispersing and resident individuals are not easily measured (Gaines and McClenaghan 1980; Greenwood and Harvey 1982; Stenseth and Lidicker 1992). Shields (1982), Waser and Jones (1983), and Waser (1988) have argued that the consequences of philopatry often receive little attention relative to the consequences of dispersal. Dispersal has been described as the “glue” which joins ecology, population genetics, ethology, and evolution (Stenseth and Lidicker 1992). Philopatry, or lack of dispersal from the natal site, is equally significant (Waser and Jones 1983). Yet natal dispersal and philopatry should be viewed as part of a continuum, with relative costs and benefits for each, depending on a host of ecological and environmental factors such as competition for limiting resources (Waser 1985), optimal inbreeding (Shields 1982), habitat heterogeneity (Cockburn 1992; Gliwicz 1992), reproductive benefits to residents (Anderson 1989), and mate competition (Dobson 1982; Moore and Ali 1984). Quantifying the
reproductive consequences of philopatry and dispersal can help in understanding the evolutionary costs and benefits of these strategies.

Evaluating fitness of philopatric and dispersing individuals has yielded mixed results in both birds and mammals. Dispersers have been shown to have higher reproductive success than philopatric individuals in bank voles (Clethrionomys glareolus) (Gliwicz 1990), prairie voles (Microtus ochrogaster) (Johnson and Gaines 1985, 1987), and great tits (Parus major) (Greenwood et al. 1979). In other species, reproductive success was similar among dispersers and philopatric individuals (Peromyscus leucopus, Wolff et al. 1988; song sparrows, Melospiza melodia, Arcese 1989). Reproductive success of female Columbian ground squirrels (Spermophilus columbianus) was lower for immigrant females than for resident females (Wiggett and Boag 1993). However, in some studies dispersal is not differentiated from death, so this potentially major cost to dispersing individuals is not measured. In addition, few authors express reproductive success as a function of distance moved from the natal site.

Waser (1988) examined the ecological conditions that favour philopatry. He argued that demographic parameters such as adult survival determine how
rapidly home range ownership changes, and that juveniles that remain on their natal area after a parent has died exhibit “opportunistic philopatry”. In contrast, philopatry is assumed to involve some form of parental “consent” if a greater proportion of juveniles remain close to the natal site than expected on the basis of annual home range turnover. Studies of many ground-dwelling sciurid species have shown that females generally remain philopatric (e.g., Michener and Michener 1977; Sherman 1977; Michener 1979, 1981, 1983; Holekamp 1984; Wiggett and Boag 1992). Yet the fitness benefits of philopatry in ground-dwelling sciurids have not been closely examined.

In this chapter, I examine the fitness of philopatric and dispersing juvenile female arctic ground squirrels (Spermophilus parryii plesius) in the boreal forest. I define emigration as the movement of a juvenile from its natal area. Emigration can be a short-distance movement, but may result in dispersal if the individual moves farther than the diameter of one average adult female home range from its natal area and remains in the new location to breed (Howard 1960; Greenwood 1980). Conversely, I consider philopatry to be minimal emigration resulting in a juvenile reaching reproductive age within one average adult female home range diameter from the natal burrow or in contact with the maternal home range (Anderson 1989; Greenwood
I use average annual fecundity (mean number of female offspring per female per year) as a measure of fitness (Wiggett and Boag 1993; Donovan et al. 1995; Hoogland 1995).

I tested the hypothesis that philopatry occurs by parental consent and is not merely opportunistic (Waser 1988). I made the following predictions:

(1) More juvenile female arctic ground squirrels would remain philopatric than expected on the basis of annual survival of adult females in the population;

(2) A frequency distribution of dispersal distances of radio-collared juvenile females would be biased toward zero, because juvenile females would be expected to remain as close as possible to the natal site;

(3) Juvenile females that dispersed more than one adult female home range diameter from their natal burrow would, on average, have lower fitness than philopatric females because of poor survival, production of fewer offspring, or both;

(4) The proportion of juvenile females dispersing would increase with population density, because fewer food resources and burrow systems would be available per capita.
Methods

Study sites

I measured emigration, dispersal, survival, and fecundity of juvenile female arctic ground squirrels on seven 9-ha experimental grids containing 100 grid points spaced 30 m apart and located in a 10x10 array: (1) four unmanipulated CONTROL grids (CONTROLS A, B, C, and D); (2) a FOOD grid provisioned \textit{ad lib} with pelleted rabbit chow (minimum 16\% crude protein) distributed by fertiliser spreader along four 600-m cut lines ("feeder rows"); (3) a PREDATOR EXCLOSURE grid contained within a 1-km\textsuperscript{2} area surrounded by an 8600-Volt electric fence to deter terrestrial predators, and partially covered by monofilament lines spaced about 30 cm apart in an attempt to deter avian predators; and (4) a PREDATOR EXCLOSURE+FOOD grid which combined both predator exclosure and food supplementation treatments as described above (also see Figure 1.1 in Chapter 1). All experimental sites were located within larger (36 ha) grids, established to manipulate snowshoe hare (\textit{Lepus americanus}) populations as part of a large-scale experiment to examine trophic linkages in the boreal forest community (Krebs \textit{et al.} 1992, 1995; Boutin \textit{et al.} 1995).
Field methods

From 1992 to 1995, juveniles on all study sites were trapped in Tomahawk live traps, tagged with Monel No. 1005-1 tags (National Band and Tag Co.) in both ears, weighed to the nearest 2 g with a Pesola spring scale, and sexed. From 1993 - 1995, 102 juvenile females were radio-collared on CONTROLS A and D, and on the three treatments, as described in Chapter 3. I located each individual once every two days with a hand-held antenna.

I measured the emigration distance of each juvenile as the straight-line distance between its place of birth (natal burrow or mother's home burrow) and its sleeping burrow in autumn prior to hibernation. Because dispersal of arctic ground squirrel females in spring is rare (Green 1977 and pers. obs.), I assumed that autumnal sleeping locations were an accurate measure of a female’s emigration distance to the core area of a newly-established home range (after Hackett 1987). I located sleeping burrows by radio-tracking sleeping individuals in the early morning before sunrise (=0700h) in late August. Females from the PREDATOR EXCLOSURE had to travel at least 146 m, whereas CONTROL females had to move a distance of at least 172 m to be classified as dispersers owing to the different home range sizes on the different treatments (Appendix IV). Emigration distances of individuals that died in their first active season
were calculated as the straight-line distance between their natal burrows and their point of death. On-grid emigration distance was calculated from the grid coordinate system. Dispersal or emigration locations of squirrels that moved beyond the study sites were determined using a Trimble Basic GPS (global positioning system). GPS coordinates obtained in the field were accurate to within approximately 20 m after being differentially corrected using a base station at the Kluane Lake Research Station.

**Estimates of fitness**

To measure mean annual fecundity, I used 34 of the 102 females that had been radio-collared as juveniles (Figure 4.1). The 34 females included: (1) females from CONTROL and PREDATOR EXCLOSURE grids that had survived to reproductive age (n=17); and (2) females from CONTROL and PREDATOR EXCLOSURE grids that either did not survive their first active season (n=10) or were not trapped in the following spring (n=7) so presumably had not survived hibernation during their first winter. Sixty-eight radio-collared juvenile females were excluded from measurements of fecundity either because they were born in 1995 (hence did not reproduce in the time frame of this study) or because they were born on food-supplemented areas, where it was difficult to assign maternity (see below).
Females that did not survive to reproductive age (n=17) each had an individual fitness of zero. For the remaining 17 females that had been radio-collared as juveniles, I calculated fecundity by re-trapping and radio-collaring each female as a yearling and in subsequent years, determining the location of her natal and home burrows, and trapping all offspring she produced. For some females, it was possible to trap and count two or three years’ offspring, but for others it was possible to count only offspring they produced as yearlings because they were born in 1994, one season before I finished my study. For this reason, I calculated the average annual fecundity (AAF) of each female by counting the total number of offspring she produced, halving this total to account for the 1:1 sex ratio at birth (Lacey 1991), and dividing by the number of years that offspring were counted (Caughley 1977). Thus,

$$\text{AAF} = (0.5*N)/Y$$

where $N$ is the total number of offspring produced by a female, and $Y$ is the number of years that a female’s offspring were counted.

This approach assumes that fecundity does not vary with a female’s age (Brown 1988). I tested this assumption by comparing 13 females from CONTROL and PREDATOR EXCLOSURE areas whose offspring were trapped and counted for
more than one year. Yearling females had a mean (± S.E.) of 2.76 ± 0.73 offspring per litter, whereas the same females as two-year-olds had a mean of 4.06 ± 0.43 offspring per litter. Although there was a trend towards older females having larger litters, this difference was not significant (Wilcoxon signed-rank test, Ts=25; n=13; p>0.05). In ground-dwelling sciurids, yearling females often have smaller litters than older females (Murie et al. 1980), although Michener (1989, 1990) reported that yearling female Richardson's ground squirrels (Spermophilus richardsonii) did not have significantly smaller litters than older females. It is likely that in arctic ground squirrels, yearling females may have slightly smaller litters than older females. However, when I used only offspring produced by yearling females as a measure of reproductive success, it made no qualitative difference to the results presented below, so I assumed that AAF was not biased by the length of time that I followed a female.

Thirty-six additional females were ear-tagged but not radio-collared in their juvenile year and followed from 1992 to 1995 (Figure 4.1). Birthplaces of these females were known. I calculated emigration and dispersal distances as for radio-collared females, using the straight-line distance between the birthplace and the core area of the female's new home range. The 17 females that had been radio-collared in their juvenile year and that survived to reproductive age were
added to this sample, to give a total of 53 females that survived to reproductive age and for which litter sizes and emigration distances could be accurately estimated (Figure 4.1).

Only females from CONTROL and PREDATOR EXCLOSURE treatments were used to measure reproductive success for two reasons. First, all females from these treatments had similar average body condition and litter sizes (Karels 1996). On treatments where food was added, litter sizes were significantly larger and females were in better condition, and thus a direct comparison was not appropriate. Second, an accurate measure of litter size was not possible for most females from food-supplemented treatments, because the higher population densities and close proximity of females on these treatments meant that juveniles from different litters mixed quickly after emergence. This problem was less common on CONTROL and PREDATOR EXCLOSURE treatments where population densities were lower. Of the 53 females that survived to reproductive age and whose litters were trapped and counted from 1992 to 1995, 33 (=62%) produced litters where maternity was unambiguous and offspring could be assigned to a particular female. The remaining 38% (20 females) shared a burrow system with another female in at least one of the four years. In all cases, the total number of offspring produced at such burrow systems was at least 8,
which considerably exceeded the mean number of offspring per female, based on counts of placental scars from a road-killed sample of dead females (mean (± S.E.) was 5.35 ± 0.82; n=23; mode=5; median=5; Appendix IX). I calculated litter sizes of these females by assigning equal numbers of offspring to each female. Although this method risks introducing some error, exclusion of females in years when they shared a burrow system did not affect the following results, so they were included in all analyses.
FIGURE 4.1. Fates of 102 juvenile female arctic ground squirrels radio-collared at emergence and used for estimating fitness on CONTROLS A and D and on the PREDATOR EXCLOSURE, 1993 to 1995. Thirty-six additional females ear-tagged from 1992 to 1995 and that survived to reproductive age were also used to estimate fitness as a function of emigration distance.
102 Females collared

68 Born in 1995 or on food-supplemented treatments; used to measure proportion dispersing from all study sites and to create a frequency histogram of dispersal distances but not used to measure fitness

34 Used to measure fitness

17 Died in first active season or first winter (fitness=0)

17 Survived to reproductive age

36 Survived to reproductive age and ear-tagged but not collared; birthplace known

53 Survived to reproductive age; fitness plotted as a function of dispersal distance
Proportion of females dispersing as a function of population density

All 102 juvenile females radio-collared on the four study sites (CONTROLS A and D, PREDATOR EXCLOSURE, FOOD, and PREDATOR EXCLOSURE + FOOD) from 1993 to 1995 were classified as either dispersing or philopatric. On each treatment, the proportion of females classified as dispersers (the dispersal frequency) was plotted against density of resident adults in spring to determine whether the proportion of juvenile females dispersing increased as population density increased.

Burrow systems as a limiting resource

To determine whether burrow availability was limiting for juvenile females, I calculated the ratio of the total number of burrow systems to the total number of adult females on CONTROL and PREDATOR EXCLOSURE areas from 1993 to 1995. I used only large perennial burrow systems with multiple entrances where I knew juveniles had been produced in at least one of the years 1992 to 1995 (pers. obs.). I assumed that if the burrow:female ratio was greater than or equal to 1, every female had a burrow system available to her for producing offspring. If the ratio was less than 1, I assumed that burrows were limiting. I did not count the number of burrow systems available on each adult female’s home range because home ranges sometimes overlapped (see results), which produced an
artificially high estimate of the number of burrow systems available per female. Hence, the approach described above should be regarded as a conservative estimate of burrow system availability.

**Adult female home range geometry**

Hubbs and Boonstra (submitted) found no relationship between home range size and population density of adult female arctic ground squirrels in the boreal forest. I found that home ranges of adult females were smaller on food-supplemented treatments, but did not change from year to year on any grid treatments from 1993 to 1995 (Appendix IV). Yet population density increased during this time, so I calculated an “index of overlap” for the CONTROL and PREDATOR EXCLOSURE areas from 1993 to 1995 by taking the ratio of the number of females on the trapping grid (determined from live-trapping data) to the average home range size. I expected this index to increase with increasing population density because home range sizes had low inter-annual variation. This approach assumes that home ranges were roughly contiguous. This was usually the case, because my study sites were located in areas of approximately similar habitat (mainly open spruce (*Picea glauca*) stands and shrub-meadow (*Salix* spp. and *Betula glandulosa*); and Boonstra, in press).
**Statistical analyses**

All analyses were done using JMP for Macintosh (SAS Institute 1994). The proportion of females classified as dispersers was compared with the expected proportion of dispersers using a G-test (Sokal and Rohlf 1995). Fecundity of the 34 radio-collared females (including the 17 females that did not survive to reproductive age) was plotted as a function of emigration distance in their juvenile year. Fecundity of the 53 females that survived to reproductive age (17 radio-collared and 36 ear-tagged but not collared) was plotted in a similar manner.

The shapes of both fitness curves were described by a smoothing spline, which uses a nonparametric regression to estimate the form of the unknown curve describing a set of data points (Eubank 1988; Schluter 1988). It fits a curve to data using local estimates of slope, and consists of several cubic polynomials joined seamlessly. Such a combination of polynomials can have a rough appearance, and for this reason a smoothing parameter, lambda (λ) is used in the equation (Eubank 1988). The optimal value for lambda minimises the sum of squared prediction errors, to give a minimal Generalised Cross-Validation (GCV) score (Schluter 1988). The lambda values reported here were chosen to minimise the GCV score for each data set.
Fecundity of females that dispersed in their juvenile year was compared with that of philopatric females using Welch's approximate t-test. Data were transformed by means of a ln(x+1) transformation (assuming unequal variances) as described in Sokal and Rohlf (1995). Fecundity of dispersing and non-dispersing females that survived to reproductive age was similarly compared with a t-test (variances were equal). The proportion of radio-collared juvenile females that dispersed plotted against adult population density on each treatment in each year was analysed using linear regression.
Results

Proportion of females dispersing

Of the 34 radio-collared females from CONTROL and PREDATOR EXCLOSURE treatments, only 4 (12%) were classified as dispersers and 30 (88%) were philopatric. From live-trapping data on CONTROL and PREDATOR EXCLOSURE areas, I calculated that, on average, approximately 47% of adult females died annually from 1992 to 1995 (through active season death or overwinter loss). Hence, if females are simply filling available spaces left vacant by adults, approximately 47% of juvenile females should have remained and 53% should have dispersed. This expected value differed significantly from the observed 88% philopatric females ($G=25.76; \chi^2=10.83; df=1; p<0.001$). Of the 53 females who survived to reproductive age, 6 (11.3%) were classified as dispersers and 47 (88.7%) as philopatric. In addition, a frequency distribution of emigration distances of all 102 juvenile females on all treatments that were radio-collared from 1993 to 1995 was strongly biased towards zero (Figure 4.2).
FIGURE 4.2. Frequency distribution of emigration distances of 102 juvenile arctic ground squirrel females radio-collared from 1993 to 1995. Arrow shows the approximate diameter of an average adult female home range.
Females radio-collared as juveniles: fitness

Fecundity of females radio-collared as juveniles is shown in Figure 4.3(a). None of the four females that dispersed survived to reproductive age. All radio-collared females that survived to produce offspring did so within one female home range diameter from their birthplace. For philopatric females, fecundity was highest if they settled 80 - 120 m from their birthplace (Figure 4.3(a)), which was approximately at the periphery of an adult female home range. Average fecundity of dispersing and philopatric females differed significantly (Table 4.1; t-test: one-tailed p<0.0001; df=29; t=4.92).

Females that survived to reproductive age: fitness

Fecundity of the 53 females that survived to reproductive age (including the 17 radio-collared females) was highest for individuals that moved 80 - 120 m from their natal burrow (Figure 4.3(b)). Females that dispersed, but survived to reproductive age, had lower fecundity than philopatric females (Table 4.1; t-test: one-tailed p<0.008; df=51; t=2.48).
FIGURE 4.3.

(a) Average annual fecundity (AAF) of 34 females that were radio-collared as juveniles as a function of emigration distance in their juvenile year. Smoothing spline fit: $\lambda=1755$; $r^2=0.38$; sum of squares error=22.59. Females that did not survive to reproductive age are included in this plot.

(b) Average annual fecundity (AAF) of 53 females that survived to reproductive age as a function of emigration distance in their juvenile year. Smoothing spline fit: $\lambda=2059$; $r^2=0.29$; sum of squares error=129.16.

Error bars are ± 1 S.E. and represent inter-annual variance in fecundity of individual females. Points without error bars had no measurable error, either because females had no inter-annual variation in fecundity or (more commonly) because fecundity was measured for only one year.
(a) Radio-collared females

Philopatric (n=30) ○
Dispersed (n=4) ●
Spline Curve; $\lambda=1755$

(b) Females that survived to reproductive age

Philopatric (n=47) ○
Dispersed (n=6) ●
Spline Curve; $\lambda=2059$

Emigration distance in juvenile year (m)
TABLE 4.1. Fecundity of dispersing and non-dispersing females.

(a) Females that had been radio-collared as juveniles (including females that did not survive to reproductive age).

(b) Females that were ear-tagged but not collared as juveniles, who survived to reproductive age and whose birthplace was known.

Numbers are average number of female offspring per female per year (± S.E.); sample sizes are shown in brackets.

<table>
<thead>
<tr>
<th>Mean number of female offspring per female per year:</th>
<th>Non-dispersers</th>
<th>Dispersers</th>
<th>Total n</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Radio-collared females, including females that died in their first active season</td>
<td>0.93 ± 0.20 (30)</td>
<td>0 ± 0 (4)</td>
<td>34</td>
</tr>
<tr>
<td>(b) Females that survived to reproductive age</td>
<td>1.47 ± 0.13 (47)</td>
<td>0.46 ± 0.16 (6)</td>
<td>53</td>
</tr>
</tbody>
</table>
Proportion of juvenile females dispersing as a function of population density

The proportion of females classified as dispersers on each of the four experimental treatments in 1993 to 1995 (measured using all 102 radio-collared females) showed little relationship with density (Figure 4.4). The highest proportion of female dispersers occurred on the PREDATOR EXCLOSURE+FOOD treatment in 1995 where population densities were highest, but where food and possibly burrow sites were limiting (Chapter 3). Inclusion of this data point resulted in a significant positive relationship between dispersal frequency and population density ($r^2=0.51$; $F=10.2$; $p<0.01$, $n=12$). At lower population densities commonly observed in the boreal forest, there was no relationship between dispersal frequency and population density ($r^2=0.03$; $F=0.29$; $p>0.60$, $n=11$) (Figure 4.4).
FIGURE 4.4.

Proportion of juvenile female arctic ground squirrels classified as dispersers on four experimental treatments from 1993 through 1995, as a function of population density of resident adults in spring. At lower population densities commonly observed in the boreal forest, there was no relationship between dispersal frequency and population density (lower line). Only females from the PREDATOR EXCLOSURE+FOOD treatment in 1995 had a high frequency of dispersal, and including this data point resulted in a significant positive relationship between dispersal frequency and population density (upper line).
Burrow system availability

The number of burrows available per female always exceeded 1 from 1993 to 1995, which suggests that females on CONTROL and PREDATOR EXCLOSURE areas were not limited by burrow availability (Table 4.2).

Home range overlap

Home range overlap of adult females increased from 1993 to 1995 on both CONTROL and PREDATOR EXCLOSURE study sites, which suggests that a higher population density of females could be accommodated by sharing resources within a home range (Table 4.2). Home range geometry in 1993 and 1995 is shown for the PREDATOR EXCLOSURE treatment (Figure 4.5). Areas plotted are 100% Minimum Convex Polygon (MCP; Jennrich and Turner 1969). Control areas showed similar qualitative changes in home range geometry.
TABLE 4.2. Number of available burrow systems per adult female and index of adult female home range overlap on CONTROL and PREDATOR EXCLOSURE grids, 1993 to 1995. I calculated the index of overlap by taking the ratio of the total number of females on each trapping grid in each year (determined from live-trapping data) to the average home range size.

<table>
<thead>
<tr>
<th></th>
<th>1993</th>
<th>1994</th>
<th>1995</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Burrow:Female ratio</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Controls</td>
<td>3.71</td>
<td>2.89</td>
<td>1.58</td>
</tr>
<tr>
<td>Pred. Exclosure</td>
<td>2.73</td>
<td>2.73</td>
<td>1.73</td>
</tr>
<tr>
<td><strong>Index of overlap</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Controls</td>
<td>3.71</td>
<td>4.26</td>
<td>11.59</td>
</tr>
<tr>
<td>Pred. Exclosure</td>
<td>5.00</td>
<td>4.64</td>
<td>9.56</td>
</tr>
</tbody>
</table>
FIGURE 4.5. Qualitative representation of the change in overlap of adult female home ranges on the PREDATOR EXCLOSURE treatment between 1993 and 1995. CONTROL areas showed similar changes. Open areas represent areas where no ground squirrels were radio-collared. OI = overlap index (from Table 4.2).
Discussion

My results provide support for the hypothesis that juvenile female arctic ground squirrels do not merely show opportunistic philopatry. Adult females either actively recruited their daughters to settle in contact with their home range, or at least, did not force them to disperse. More juvenile females were philopatric than expected on the basis of annual adult female mortality. Philopatric female arctic ground squirrels had higher fecundity than females that dispersed beyond one adult female home range from their natal area. In addition, adult female arctic ground squirrels may have tolerated juvenile female philopatry by allowing an increase in home range overlap as densities increased, which ensures that their daughters remained in contact with the maternal range.

Dispersal and population density

Animals may disperse because of competition for resources such as food or burrow systems at high population densities. I found little relationship between female dispersal and population density except for one study site (the PREDATOR EXCLOSURE+FOOD treatment in 1995). In this case, population densities were artificially high (17x those of controls) as a result of
several years of supplemental food and protection from predators (Chapter 2). Hence, burrow systems and natural food may have been limiting.

Murray (1967) presented a graphical model which suggested that it is selectively advantageous for animals to move no farther than the first uncontested site they find. Waser (1985) extended Murray’s ideas and described two models predicting the distribution of dispersal distances as a function of the number of home ranges becoming vacant annually. He suggested that competition for resources was probably driving dispersal (individuals moved to the first available space, thereby producing a skewed distribution in dispersal distances). He also argued that other factors influencing dispersal, such as inbreeding avoidance and habitat selection, would deviate from the skewed distribution. These deviations could be detected statistically. Rodgers and Klenner (1990) developed a simulation model of Murray’s (1967) hypothesis and argued that competition for resources is a sufficient explanation for many observed skewed distributions of dispersal distance. My results also suggest that juvenile females are moving the shortest possible distance before settling.
Yet if competition for resources is “the primary factor driving dispersal” (Waser 1985), why did I not observe a stronger relationship between population density and female dispersal tendency? The unusually high frequency of female dispersal from the PREDATOR EXCLOSURE+FOOD treatment in 1995 suggests that, at very high densities, females may disperse for this reason. Possibly, dispersal tendency is not related to density in a linear fashion. The relationship may be strongly curvilinear, resulting in dispersal of females only at very high densities. This may be analagous to Lidicker’s “saturation dispersal” models (Lidicker 1975; Stenseth and Lidicker 1992). A similar relationship was suggested by Garrett and Franklin (1988) to explain black-tailed prairie dog (Cynomys ludovicianus) dispersal patterns. In my study, population densities were low but increasing from 1992 through 1995 (Chapter 2), and overlap of adult female home ranges also increased. The above models assume no overlap in home range, so the flexibility of arctic ground squirrel females in sharing home ranges may explain why I saw little relationship between female dispersal rates and density.

Similar changes in home range geometry have been observed in round-tailed ground squirrels (S. tereticaudus) (Dunford 1977), S. richardsonii (Michener 1979, 1981), S. columbianus (Festa-Bianchet and Boag 1982), P. leucopus
(Wolff and Lundy 1985), and kangaroo rats (*Dipodomys spectabilis*) (Waser 1988). Hence, female offspring are likely to reside close to their parents, particularly if resources are not limiting and females are not forced to disperse. During the increase and peak phases of the snowshoe hare (*Lepus americanus*) cycle, when arctic ground squirrels may reach higher population densities (as they were in 1991; Chapter 2), food and burrow systems may possibly become limiting and more juveniles may be forced to disperse. Conversely, it is possible that arctic ground squirrel populations at Kluane never reach densities where females would disperse in large numbers because of the increase in predator numbers (and hence, increased predation on arctic ground squirrels) as a consequence of the snowshoe hare cyclic increase (Chapter 2).

**Reproductive success of dispersers and non-dispersers**

Gliwicz (1990) observed higher reproductive success in dispersing *C. glareolus* than in philopatric individuals, but she noted that without an estimate of survival during dispersal, it was impossible to say whether dispersing individuals had higher fitness (Gliwicz 1992). Wolff and Lundy (1988) found that reproductive success of immigrant *Peromyscus* was the same as that of natal residents, whereas Wiggett and Boag (1993) found reproductive
success of immigrant female *S. columbia*us to be lower than for natal residents. Again, survival of dispersers and non-dispersers was not quantified before fecundity was measured.

In my study, the few female arctic ground squirrels that dispersed had lower fecundity (and therefore presumably fitness) than those that were philopatric. None of the 34 radio-collared females that survived to reproductive age dispersed more than one average female home range diameter from her birthplace. The sample size of dispersing females (*n*=4) was small, but two lines of evidence suggest that high mortality of dispersers was common for juvenile female arctic ground squirrels. First, four years of trapping and recapturing juveniles on CONTROL and PREDATOR EXCLOSURE treatments yielded only six females classified as dispersers (out of approximately 85 ear-tagged females) that survived to reproductive age (Figure 4.3(b)). Second, only 2 of 12 dispersing radio-collared juvenile females from the FOOD and PREDATOR EXCLOSURE+FOOD treatments survived to reproductive age. One of these two females failed to produce offspring as a yearling. The other female dispersed off the FOOD treatment and was followed for two subsequent years. During this time period I trapped and counted all her offspring. She did not share a burrow system
with any other females. She produced 3 offspring as a yearling and none in the following year. The cost of dispersal (in the form of a high risk of mortality) appeared to be high.

Even if a dispersing female survives to reproductive age, she is likely to have lower fitness than a philopatric female (Figure 4.3(b)). Several behavioural mechanisms described for ground-dwelling sciurids (Holekamp 1986) and voles (Mappes et al. 1995) may explain this observation. Dispersing juvenile females may have had stressful agonistic encounters with their siblings and resident parents, as observed in S. elegans (Pfeifer 1982) and in S. columbianus (Wiggett and Boag 1992). Further, these females may be subject to more agonistic encounters as they move beyond the natal site and encounter aggressive unrelated females, as in S. richardsonii (Michener and Sheppard 1972; Michener 1973), in S. tereticaudus (Dunford 1977), and in S. beldingi (Sherman 1981). Agonistic interactions may reduce a female’s fecundity, as was observed in C. glareolus by Mappes et al. (1995), where competition for space was most intense among unrelated neighbouring voles and lowered reproductive success. In addition, Wiggett and Boag (1993) found that annual reproductive success was higher for resident female Columbian ground squirrels than for females that subsequently immigrated to a study colony.
Does the decline in fitness I observed at \( \approx 50 \text{ m} \) from the natal burrow reflect a true decline (Figure 4.3(a))? Data presented here should be viewed as just one index of fitness. Hoogland (1995) has amassed a large amount of behavioural and demographic data on several aspects of annual and lifetime reproductive success of black-tailed prairie dogs. He found that different measures of reproductive success (e.g., number of successful copulations, number of emergent offspring, and number of offspring surviving to yearling age) were closely correlated. Further work should focus on measuring other fitness traits (e.g., those listed above) in ground-dwelling sciurids simultaneously. Such an approach would ensure that observed trends in fitness curves are real and not simply a result of too few data.

A second approach would be to study individuals in a longitudinal fashion to measure lifetime reproductive success, as advocated by Clutton-Brock (1988) and Brown (1988). Such studies often take several years (e.g., Smith 1988; Arcese 1989), but have the advantage of documenting all offspring produced by a particular individual. Observed trends in fitness curves would then be more convincing. A conservative interpretation of the data observed in my study is that surviving philopatric females have a good chance of producing
some offspring if they remain in contact with their mother’s range and that fitness may decline because of poor survival and reduced fecundity if females disperse to a point where they are surrounded by aggressive, less related adult females.

Two mechanisms may explain the observation that slightly higher fitness occurred in the range 80 - 120 m from the natal burrow: (1) Juvenile females may be moving to the location of “least resistance” in the form of agonistic encounters with resident adults, and adult females did not actively recruit their juvenile female offspring to the periphery of their home range; (2) Adult females practised a form of “bequeathal”, where female offspring were allowed to settle in contact with the resident adult’s home range (i.e. philopatry was by “parental consent” in Waser’s (1988) sense). The latter possibility is supported by two pieces of evidence. First, “regular” bequeathal (complete abandonment of the home range to offspring during the breeding season; Harris and Murie 1984; Cockburn 1992) was rarely observed in boreal forest arctic ground squirrel populations, and adult females had high site fidelity (as they do in alpine tundra; Green 1977). Hence, adult females were probably either sharing burrow systems with their daughters, or allowing them to take over burrow systems within their home range, or a
combination of both, but were not relinquishing burrow systems to their daughters as Harris and Murie (1984) observed in *S. columbianus*.

Second, many of the adult females whose juveniles were radio-collared were themselves radio-collared and occasionally it was possible to radio-track both a female and her offspring. Each year, three or four adult females were observed moving with their radio-collared juvenile(s), often staying in an unfamiliar burrow system with offspring for one to three days before returning to the original natal site. Festa-Bianchet and Boag (1982) suggested that adult female territoriality in *S. columbianus* evolved to protect juveniles from attacks by unrelated adult females. In arctic ground squirrels, females may be maximising fitness by allowing daughters to settle at the periphery of their home range, thereby providing them with optimal resources for their own reproduction.

Many studies of dispersal have been plagued by distance-weighted sampling methods. Porter and Dooley (1993) examined 15 studies that were used to validate models of dispersal movements (e.g., Waser 1985, Buechner 1987). In 14 of the 15 studies, the field data consisted of point- or plot-based sampling within a specific area. Porter and Dooley (1993) argued that if
animals fail to encounter an observation point, or move beyond the edges of a plot, their movements are not always detected. They emphasised that field studies of animal movement must sample equally over distance to avoid this problem. They recommended radio-tracking as a useful technique for assessing individual movements equally over all distances. In my study, two of 102 juvenile females that were radio-collared at emergence were lost permanently. With such a low proportion of juvenile females lost in a 3-year period, the skewed distribution I observed is almost unbiased.

**Future investigation of the fitness consequences of dispersal and philopatry**

The relative costs and benefits of dispersal for juveniles of both sexes should be further investigated. Density-dependent dispersal was strong but non-linear in this study, although a more linear relationship was observed over a broader range of population densities in *S. columbianus* (Wiggett and Boag 1992). Further insight into the relationship between population density and female dispersal in arctic ground squirrels could focus on a wider range of arctic ground squirrel population densities in the boreal forest to examine the exact nature of the relationship between population density and dispersal in this species. This is a realistic objective because arctic ground squirrel
populations fluctuate in response to changes in predation intensity as a result of the snowshoe hare cycle (Chapter 2).

Future studies of reproductive success of dispersing and philopatric females could focus on habitat quality and heterogeneity as factors affecting the quality of a female’s natal environment, and hence the decision to emigrate from the natal area. Waser (1988) concluded that food and nest sites were probably not limiting to *Dipodomys spectabilis* in a similar study, but cautioned that his study was carried out during a period of low population density. In my study also, population densities were low but increasing (Chapter 2). Hence, juvenile females generally did not disperse away from study areas into poor quality habitat. However, at higher population densities, they may be forced to do so.

A further test of the hypothesis that philopatry is not merely opportunistic could involve removal of adult females or siblings to observe juvenile female philopatry under these experimental conditions. It may also be possible to examine the fitness constraints of true bequeathal, compared with the form of bequeathal observed in this study where female offspring appeared to have highest fitness if they emigrated to the periphery of their mother’s home range. Further, there is evidence that
successful female *S. richardsonii* (measured by noting the number of their descendants present in a population in subsequent years) may produce female-biased litters (Michener 1980). Similar sex-biases in litter production were observed in thirteen-lined ground squirrels (*S. tridecemlineatus*) (McCarley 1970) and in Townsend’s voles (*Microtus townsendii*) (Lambin 1994). It would be interesting to examine sex-bias in litters of dispersing and philopatric females.

Finally, I emphasise that in this chapter I have examined the fitness costs and benefits of dispersal and philopatry for females only. Future work should similarly investigate reproductive costs and benefits of dispersal for males, particularly in polygynous rodent species where male dispersal appears to incur a high mortality cost, but where successful dispersal may lead to very high reproductive success via successful mating with many females.
Summary

I studied emigration, dispersal, survival, and fecundity of 70 female arctic ground squirrels (*Spermophilus parryii plesius*) in the boreal forest at Kluane, Yukon Territory from 1992 to 1995. I tested the hypothesis that philopatry is not merely opportunistic, but occurs by parental consent. I predicted that females that dispersed farther than one adult female home range diameter from their birthplace would have lower fitness than those that stayed close to their natal range.

Juvenile females were predominantly philopatric, and the proportion of females that remained philopatric was greater than expected given the annual survival rate of adult females (from which the number of available home ranges could be estimated). Females that dispersed more than one mean adult female home range diameter from their birthplace reared fewer female offspring, on average, than females that were philopatric. Highest fitness was achieved for females at distances similar to the average home range diameter of an adult female. My results provide evidence that dispersal out of contact with the mother’s home range results in lowered reproductive success for juvenile female arctic ground squirrels.
The proportion of juvenile females emigrating from four study populations showed no relationship with population density in any year when densities were like those commonly observed in the boreal forest. Resident adult females appeared to maximise fitness by allowing daughters to settle at the periphery of their home range, resulting in an increase in home range overlap as population density increased.
**Literature cited**


CHAPTER 5: CONCLUDING DISCUSSION - ARCTIC GROUND SQUIRRELS AND THE SNOWSHOE HARE CYCLE

Introduction

The persistence of matrilines and the social behaviour of adult females can be critical in determining population dynamics and inter-annual variation in populations of social ground-dwelling sciurids (Armitage 1981, 1984; Michener 1983; Hoogland 1995). Processes such as dispersal and philopatry can be viewed as the behaviour of individual organisms that have demographic and genetic consequences for the population as a whole (Gaines and McClenaghan 1980; Waser and Jones 1983; Hackett 1987).

Four observations from this study suggest that annual survival and fecundity of adult and juvenile females may be important in determining population fluctuations in arctic ground squirrels in the boreal forest:

(1) The strong positive relationship between adult survival and the finite rate of population increase, and the increase in population density in years of high adult survival (1993 - 1995) (Chapter 2);

(2) Most juvenile females were philopatric and had higher survival than juvenile males in their first active season (Chapter 3);
(3) Philopatric females had higher fitness, on average, than females that dispersed (Chapter 4);

(4) The increase in overlap of adult female home ranges with increasing population density which allowed most juvenile females to remain near their natal site (Chapter 4).

With these observations in mind, I examined the influence of various demographic parameters on annual rates of population change. In this chapter I present results from a stage-based simulation model of arctic ground squirrel populations at Kluane, which I used to determine sensitivity of \( r \), the rate of population change, to various demographic parameters. I will finish with a brief synthesis of our knowledge of populations of arctic ground squirrels in the boreal forest and their fluctuations as a result of the snowshoe hare cycle.

**Simulation model: sensitivity of instantaneous rate of population change to demographic parameters**

The purpose of this model was to simulate an arctic ground squirrel population with an annual cycle similar to that observed in the boreal forest at Kluane. The model was a simplified version of a real system and was designed to enable me to explore the sensitivity of \( r \), the instantaneous rate of population change, to several demographic parameters. This technique is
often employed when data are available for a particular system, and a synthesis is needed to identify uncertainties about that system (Caughley 1987; Manly 1990; Hilborn *et al.* 1995). I did not use the model to make any predictions about absolute values of population density, rates of population change, or survival, but rather to explore the impact of the following demographic parameters on rates of population change:

(1) Active season survival of each age-sex class;
(2) Litter size;
(3) Overwinter adult survival;
(4) Overwinter juvenile survival;
(5) Survival of juveniles below ground between birth and emergence.
Methods

The model was created in Excel version 5.0. The annual cycle of activity and hibernation was compartmentalised into twelve one-month periods, with population density of adults and juveniles calculated monthly and multiplied by the appropriate survival parameter (as listed above). Adult arctic ground squirrels were assumed to have a five-month active season ("summer"; April - August) and a seven-month overwinter season ("winter"; September - March) (Figure 5.1).

Juvenile arctic ground squirrels were “born” in May, their quantity being a function of the density of adult females in the population. Juveniles remained below ground for one month (June) and were then assumed to have a three-month active season (July - September) and a six-month overwinter season (October - March). Juveniles that survived overwinter were recruited into the adult population at the beginning of the adult active season in April (Figure 5.1).
FIGURE 5.1. Flow diagram of a simulation model of arctic ground squirrel populations at Kluane.
Year 1
April  Adult active season begins
May
June  monthly adult active season survival (males and females)
July
August
September  Adult overwinter begins
October
November  monthly adult overwinter survival
December
January
February
March
Year 2
April  Adult active season begins ... etc.

Juveniles from previous year recruited to adult population
Juveniles "born" as a function of adult female population density
Juveniles below ground for one month before emergence

monthly juvenile active season survival (males and females)
monthly juvenile overwinter survival

Juveniles recruited to adult population ... etc.
Squirrel population density was calculated in May of each year by adding the separate population densities of adult males and females. The instantaneous rate of population change was calculated as $r = \ln\frac{N(t+1)}{N(t)}$ each year.

The initial demographic parameters listed in Table 5.1 represent approximate mean monthly values that I observed in arctic ground squirrel populations at Kluane from 1990 - 1995 (Appendix II). Below-ground juvenile survival was calculated by Karels (1996). Each of these parameters was varied individually while all others were held constant. I varied parameter values by increasing or decreasing them ±10%, ±20%, ±30%, etc. of the mean value. For example, I increased litter size from 4.0 to 4.4 (+10%), to 4.8 (+20%), and so on, and decreased litter size from 4.0 to 3.6 (-10%), to 3.2 (-20%). Below ground juvenile survival was increased from 0.75 to 0.83 (+10%), to 0.90 (+20%), and so on. Similar treatment was applied to all parameters. In some cases (for adult and juvenile female monthly survival, for example), it was necessary to increase or decrease parameter values by 1% increments. Each time I changed the value of a parameter, I ran the model for approximately 20 years or until $r$ reached an asymptote.
TABLE 5.1. Initial values of demographic parameters used in the simulation model for sensitivity analysis. Initial density of adult males was assumed to be 0.5 squirrels/ha, and initial density of adult females was assumed to be 2.0 squirrels/ha. Demographic parameters shown were within the range of values observed in control populations of arctic ground squirrels in the boreal forest at Kluane. A complete summary of demographic parameters is shown in Appendix II.

<table>
<thead>
<tr>
<th>Demographic parameter</th>
<th>Mean value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Litter size</td>
<td>4</td>
</tr>
<tr>
<td>Below-ground juvenile survival (one month)</td>
<td>0.75</td>
</tr>
<tr>
<td>Monthly survival adult males</td>
<td>0.9</td>
</tr>
<tr>
<td>Monthly survival adult females</td>
<td>0.9</td>
</tr>
<tr>
<td>Monthly survival juvenile males</td>
<td>0.6</td>
</tr>
<tr>
<td>Monthly survival juvenile females</td>
<td>0.75</td>
</tr>
<tr>
<td>Monthly overwinter adult survival</td>
<td>0.95</td>
</tr>
<tr>
<td>Monthly overwinter juvenile survival</td>
<td>0.9</td>
</tr>
</tbody>
</table>
**Results**

The instantaneous rate of population change was sensitive to the demographic parameters listed above, in the following order:

1. Survival of adult females during the active season;
2. Survival of juvenile females during the active season;
3. Survival of adults overwinter;
4. Litter size and survival of juveniles below ground (equal);
5. Survival of juveniles overwinter;
6. Survival of juvenile males during the active season;
7. Survival of adult males during the active season.

The instantaneous rate of population change was most sensitive to adult and juvenile female survival during the active season. For example, a 5% increase in active season survival of adult females resulted in a five-fold increase in \( r \), and a 5% decrease in active season survival of adult females resulted in a five-fold decrease in \( r \), producing an extremely steep slope when \( r \) was plotted as a function of the percent change in each demographic parameter (Figure 5.2). A change of \( \pm 5\% \) in survival of adult males during the active season produced very little change in \( r \), and a change of \( \pm 5\% \) in overwinter survival produced a moderate change in \( r \) (Figure 5.2).
FIGURE 5.2. Instantaneous rate of population change, r, as a function of the percent change in each of the demographic parameters listed in Table 5.1. AFS = adult female monthly survival during the active season; JFS = juvenile female monthly survival during the active season; OWAS = monthly overwinter survival of adults; LS = litter size; BGJS = below ground juvenile survival (for one month in June); and OWJS = monthly overwinter survival of juveniles. Slopes for adult and juvenile male monthly survival during the active season are not shown. However, the effect of these two parameters on r was very small, and their slopes were shallow.
Instantaneous rate of population change, $r$

% change in demographic parameter
Discussion

Observations from the model

I did not use this model to determine absolute values of instantaneous rates of population change, survival, or population density. However, I wanted to examine the sensitivity of arctic ground squirrel populations to changes in various demographic parameters, and to rank these parameters in order of sensitivity, within the range of values commonly observed in arctic ground squirrel populations in the boreal forest.

With these caveats in mind, two general conclusions can be made from the model:

(1) Population growth and decline are highly sensitive to adult and juvenile female survival during the active season, probably because females influence population trends both directly, by contributing to population density, and indirectly, by producing juveniles.

(2) Population growth and decline was also moderately sensitive to overwinter survival of adults and juveniles. Hence, a severe winter may add a stochastic element to determining trends in arctic ground squirrel populations in the boreal forest, as Hubbs and Boonstra (in press) observed in populations of arctic ground squirrels at Kluane in winter 1991 - 1992.
Arctic ground squirrel populations in the boreal forest, 1990 to 1995

Much of the range of the arctic ground squirrel is in arctic and alpine tundra regions of North America and Siberia (Nadler et al. 1974; Nadler and Hoffmann 1977). Consequently, our understanding of the population ecology of the arctic ground squirrel came from research done in arctic and alpine tundra habitats (Carl 1971; Green 1977; Batzli and Sobaski 1980) or in open meadows (McLean 1983, 1985; Lacey 1991).

Population densities of arctic ground squirrels on our control sites (maximum 2.92 squirrels/ha in summer 1991) never reached the densities described by McLean (1983) (3 - 10 squirrels/ha) and Green (1977) (5.8 squirrels/ha) in meadow and alpine tundra sites respectively. Arctic ground squirrel populations in the boreal forest are food-limited, and it is possible that forest habitats have a lower carrying capacity for arctic ground squirrels than meadow and alpine tundra sites. However, forest populations also showed a periodic decline as a result of the cyclic snowshoe hare fluctuation. Hence, during the low phase of the snowshoe hare cycle when predator populations were also low, arctic ground squirrel population densities increased more than four-fold between spring 1993 (0.54 squirrels/ha on control sites) and summer 1995 (2.75 squirrels/ha). Such regular declines and increases are not commonly observed in tundra habitats, which are characterised by a high
degree of stability over time (Carl 1971). Arctic ground squirrels have a lower annual reproductive rate than snowshoe hares, and as a consequence the maximum possible rate of increase in a boreal forest arctic ground squirrel population would be a 3-fold increase annually, assuming that the average number of offspring per litter is approximately 4 and mortality is negligible. By comparison, a snowshoe hare population can increase annually by as much as 8-fold. The cyclic fluctuation of snowshoe hares and their predators in the boreal forest provided an opportunity to examine the mechanism behind the increase in arctic ground squirrel populations from 1992 to 1995.

Arctic ground squirrels are the third highest mammalian prey biomass in the boreal forest after red squirrels and snowshoe hares, yet relatively little was known about their population dynamics in the boreal forest before we began monitoring their population densities in 1990 as part of the Kluane Boreal Forest Ecosystem Project (Hubbs and Boonstra, in press; Karels 1996). From 1990 to 1995 (the peak and decline phases of the snowshoe hare cycle) Hubbs (1994) and Hubbs and Boonstra (in press) showed that food was the major external factor limiting arctic ground squirrel populations. Predation as a limiting factor became increasingly important in arctic ground squirrel populations in 1992 and 1993 as snowshoe hare populations declined to low levels and as predators switched to arctic ground squirrels (Hubbs and Boonstra, in press; Rohner 1994; O'Donoghue 1997). Karels (1996)
demonstrated the importance of food in influencing litter sizes, percentage of females lactating, and percentage of females raising a litter to emergence, but he also concluded that predation and food interact to limit arctic ground squirrel populations during the low phase of the snowshoe hare cycle (1993 and 1994). Viewed as a long-term trend, food and predation probably interact to limit arctic ground squirrel populations during the peak, decline, and low phases of a snowshoe hare cycle. I also extended these findings to demonstrate the influence of food and predation on survival, dispersal, philopatry, and fecundity of juvenile arctic ground squirrels, and the influence of these processes on population dynamics.

Patterns of female philopatry and fecundity in arctic ground squirrel populations in the boreal forest

Juvenile female arctic ground squirrels survived better than juvenile males, and juvenile females were likely to remain in contact with their natal site once they reached reproductive maturity. In addition, fecundity of females that remained philopatric was higher, on average, than females that dispersed beyond the possible protection of their mother’s home range. The pattern of population increase observed from 1992 to 1995 was facilitated by an increase in adult female home range overlap, allowing adult females to retain their daughters on their natal area. In arctic ground squirrels, there may be strong selection for a female to remain near her natal area to raise offspring. This
was suggested by Wiggett and Boag (1993), who observed lower reproductive success in Columbian ground squirrel females that immigrated to a study colony compared with resident females.

The simulation model allowed me the opportunity to examine what would happen to population trends if various demographic parameters increased or decreased. Population trends were most sensitive to adult and juvenile female survival, which suggests a scenario where population densities can increase quickly if female survival is high and can sustain a positive rate of population growth because of the high degree of flexibility in adult female home range overlap and philopatry in the juvenile female cohort in all years.

The use of space by adult female ground-dwelling sciurids has received a great deal of attention. Armitage (1981) and Michener (1983) both linked the evolution of sociality in ground-dwelling sciurids to a continuation of reproductive investment beyond weaning, and hence, retention of daughters near the natal site by adult females. Several authors have suggested that an increase in home range overlap between mothers and their female offspring may allow adult females to protect juveniles and yearlings from agonistic behaviour directed toward them by unrelated or distantly related females (Sherman 1977, 1981; Michener 1979, 1981, 1983; Festa-Bianchet and Boag 1982; Armitage 1984). In arctic ground squirrels, patterns of space use by
adult females in the population facilitated juvenile female recruitment to the natal area. As a consequence, there was little relationship between dispersal frequency of juvenile females and population density.

During my study, overwinter losses were negligible, although Hubbs and Boonstra (in press) suggested that the high overwinter loss in winter 1991-1992 contributed to the decline in arctic ground squirrel populations immediately following the snowshoe hare decline. If so, overwinter loss introduces a somewhat stochastic element into the population ecology of this species. The rate of population change in the simulation model was moderately sensitive to poor overwinter survival. Thus, arctic ground squirrel population trends in the boreal forest may vary in susceptibility to overwinter loss, depending on the phase of the snowshoe hare cycle and concurrent patterns of active season survival of adult and juvenile females.
Conclusion

Population dynamics may be influenced by the consequences of mortality, reproduction, and dispersal for individuals. Because of the cyclic increase and decline of predators as a consequence of the snowshoe hare cycle, arctic ground squirrel populations showed a corresponding increase (1990 and 1991), decline (1992 to 1994) and increase again (1994 and 1995). Hence, predators limited arctic ground squirrel populations, and probably acted interactively with food during this time. For this reason, arctic ground squirrel populations in the boreal forest may never reach densities where juvenile females would disperse in response to resource limitation or population density. Recruitment of juvenile females is high and adult females generally retain their daughters near the natal site if possible. Hence, arctic ground squirrel populations can sustain a positive rate of population increase during the low phase of the snowshoe hare cycle, particularly if active season survival of females, and adult overwinter survival, are high.


Literature cited


APPENDIX I. An expandable radio collar for juvenile arctic ground squirrels.

Schematic diagram of the expandable radio collar I used for juvenile arctic ground squirrels, modified from a design used by M. O’Donoghue (pers. comm.) for juvenile snowshoe hares. Collars were constructed of a ≈20 cm length of 1.5 cm-wide nylon webbing, with foam rubber glued to the inside to allow neck growth. Transmitter and collar together weighed approximately 6 g. (a) Before placement on a squirrel. Arrows show positions of holes in the webbing, used for sizing to individual squirrels. (b) After placement on a squirrel. I used a cable tie to hold the two ends of the webbing together in such a way as to fit snugly around the neck of a squirrel.
APPENDIX II. Tables of demographic parameters in arctic ground squirrel populations, 1990 to 1995.
TABLE 1. Population densities of arctic ground squirrels (number of squirrels per hectare) on all experimental treatments and controls, 1990 to 1995.

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
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<tbody>
<tr>
<td><strong>Spring 1990</strong></td>
<td>2.02</td>
<td>1.48</td>
<td></td>
<td></td>
<td>1.56</td>
<td>6.96</td>
<td></td>
<td>1.76</td>
</tr>
<tr>
<td><strong>Summer 1990</strong></td>
<td>1.11</td>
<td>1.36</td>
<td></td>
<td></td>
<td>0.33</td>
<td>4.26</td>
<td></td>
<td>6.54</td>
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<td>1.72</td>
<td>2.59</td>
<td></td>
<td></td>
<td>4.78</td>
<td>9.76</td>
<td></td>
<td>4.79</td>
</tr>
<tr>
<td><strong>Summer 1991</strong></td>
<td>1.52</td>
<td>4.32</td>
<td></td>
<td></td>
<td>5.00</td>
<td>15.20</td>
<td></td>
<td>12.35</td>
</tr>
<tr>
<td><strong>Spring 1992</strong></td>
<td>0.71</td>
<td>1.36</td>
<td>0.56</td>
<td></td>
<td>1.33</td>
<td>3.70</td>
<td></td>
<td>6.91</td>
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<tr>
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<td>5.39</td>
<td></td>
<td></td>
<td>12.84</td>
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<tr>
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<td>0.96</td>
<td>0.55</td>
<td>0.33</td>
<td>1.33</td>
<td>2.22</td>
<td>2.40</td>
<td>4.71</td>
</tr>
<tr>
<td><strong>Summer 1993</strong></td>
<td>1.56</td>
<td>1.23</td>
<td>1.90</td>
<td>1.33</td>
<td>2.67</td>
<td>4.22</td>
<td>3.10</td>
<td>19.14</td>
</tr>
<tr>
<td><strong>Spring 1994</strong></td>
<td>0.70</td>
<td>0.75</td>
<td>0.69</td>
<td>0.67</td>
<td>1.67</td>
<td>2.67</td>
<td>1.89</td>
<td>9.38</td>
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<td>2.30</td>
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<td>1.51</td>
<td>0.89</td>
<td>4.40</td>
<td>6.89</td>
<td>6.75</td>
<td>27.90</td>
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<tr>
<td><strong>Spring 1995</strong></td>
<td>1.80</td>
<td>0.62</td>
<td>1.20</td>
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<td>3.10</td>
<td>5.44</td>
<td>2.90</td>
<td>19.60</td>
</tr>
<tr>
<td><strong>Summer 1995</strong></td>
<td>3.30</td>
<td>1.60</td>
<td>3.40</td>
<td>3.00</td>
<td>10.10</td>
<td>18.90</td>
<td>5.10</td>
<td>45.60</td>
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</table>
TABLE 2. Twenty-eight day active season survival of adult arctic ground squirrels, 1992 to 1995. Numbers in brackets are 95% confidence limits.

<table>
<thead>
<tr>
<th></th>
<th>Controls pooled</th>
<th>P.Ex.</th>
<th>Foods 1 &amp; 2 pooled</th>
<th>P.Ex.+Food</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>0.79 (0.74-0.83)</td>
<td>0.81 (0.76-0.87)</td>
<td>0.70 (0.66-0.74)</td>
<td>0.66 (0.61-0.71)</td>
</tr>
<tr>
<td>1993</td>
<td>0.71 (0.00-0.92)</td>
<td>0.89 (0.78-0.97)</td>
<td>0.88 (0.77-0.96)</td>
<td>0.97 (0.94-1.00)</td>
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<tr>
<td>1994</td>
<td>0.97 (0.92-1.00)</td>
<td>0.95 (0.85-1.00)</td>
<td>1.00 (1.00-1.00)</td>
<td>1.00 (1.00-1.00)</td>
</tr>
<tr>
<td>1995</td>
<td>0.88 (0.73-0.98)</td>
<td>0.97 (0.93-1.00)</td>
<td>1.00 (1.00-1.00)</td>
<td>1.00 (1.00-1.00)</td>
</tr>
<tr>
<td>1992 to 1995 combined</td>
<td>0.84 (0.59-1.00)</td>
<td>0.90 (0.71-1.00)</td>
<td>0.90 (0.82-0.97)</td>
<td>0.91 (0.86-0.95)</td>
</tr>
</tbody>
</table>
TABLE 3. Twenty-eight day active season survival of juvenile arctic ground squirrels, 1993 to 1995. Both sexes were combined for this analysis. Numbers in brackets are 95% confidence limits.

<table>
<thead>
<tr>
<th></th>
<th>Ctrls. A &amp; D pooled</th>
<th>P.Ex.</th>
<th>Food 1</th>
<th>P.Ex.+Food</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>0.91 (0.71-1.00)</td>
<td>0.68 (0.42-0.83)</td>
<td>0.81 (0.63-0.94)</td>
<td>0.92 (0.74-1.00)</td>
</tr>
<tr>
<td>1994</td>
<td>0.74 (0.47-0.91)</td>
<td>0.80 (0.62-0.93)</td>
<td>0.93 (0.85-1.00)</td>
<td>0.96 (0.87-1.00)</td>
</tr>
<tr>
<td>1995</td>
<td>0.81 (0.58-0.97)</td>
<td>0.97 (0.90-1.00)</td>
<td>0.87 (0.73-0.98)</td>
<td>0.52 (0.00-0.76)</td>
</tr>
<tr>
<td>1993 - 1995 combined</td>
<td>0.82 (0.48-0.90)</td>
<td>0.80 (0.58-0.87)</td>
<td>0.87 (0.76-0.93)</td>
<td>0.77 (0.00-0.88)</td>
</tr>
</tbody>
</table>
TABLE 4. Twenty-eight day active season survival of juvenile arctic ground squirrels in the boreal forest, 1993 to 1995. Survival estimates for both sexes are shown.

<table>
<thead>
<tr>
<th>Year</th>
<th>Males</th>
<th>Females</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ctrl. A &amp; D pooled</td>
<td>P. Ex.</td>
<td>Food 1</td>
<td>P. Ex.+Food</td>
</tr>
<tr>
<td>1993</td>
<td>0.50</td>
<td>0.37</td>
<td>0.50</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>0.83</td>
<td>0.74</td>
<td>0.78</td>
<td>0.67</td>
</tr>
<tr>
<td>1994</td>
<td>0.67</td>
<td>0.53</td>
<td>0.60</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td>0.61</td>
<td>0.86</td>
<td>0.95</td>
<td>1.00</td>
</tr>
<tr>
<td>1995</td>
<td>0.53</td>
<td>0.86</td>
<td>0.71</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>0.78</td>
<td>1.00</td>
<td>0.79</td>
<td>0.49</td>
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</table>
TABLE 5. Average litter sizes (± S.E.) of arctic ground squirrel females on four control and three experimental treatments in the boreal forest, 1991 to 1995. Data from 1991 are used with permission from Hubbs and Boonstra (submitted). Litter sizes without standard errors were calculated by taking the total number of juveniles produced on the grid and dividing by the total number of females on the grid. This approach was taken on the FOOD and PREDATOR EXCLOSURE+FOOD grids because litters began mixing quickly after emergence and maternity was ambiguous. Numbers in brackets are sample sizes.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1991</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.4 (18)</td>
<td>3.0 (14)</td>
<td>3.0 (39)</td>
<td>1.6 (30)</td>
</tr>
<tr>
<td>1992</td>
<td>1.3±0.8 (4)</td>
<td>0±0 (1)</td>
<td>0.7±0.5 (6)</td>
<td>0.6±0.3 (11)</td>
<td>2.5 (8)</td>
<td>1.5 (27)</td>
<td>1.4 (29)</td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td>2.7±0.8 (6)</td>
<td>0±0 (2)</td>
<td>5.5±0.5 (2)</td>
<td>3.0±0 (2)</td>
<td>2.8±0.6 (12)</td>
<td>2.6±0.8 (11)</td>
<td>3.2 (12)</td>
<td>4.8 (16)</td>
</tr>
<tr>
<td>1994</td>
<td>2.3±0.6 (9)</td>
<td>0±0 (4)</td>
<td>1.8±0.6 (4)</td>
<td>1.3±0.8 (4)</td>
<td>1.6±0.3 (21)</td>
<td>3.8±0.6 (15)</td>
<td>4.1 (16)</td>
<td>5.1 (25)</td>
</tr>
<tr>
<td>1995</td>
<td>2.3±0.6 (12)</td>
<td>4.3±1.2 (12)</td>
<td>2.6±0.5 (7)</td>
<td>3.9±0.6 (7)</td>
<td>3.0±0.3 (29)</td>
<td>3.7±0.3 (15)</td>
<td>5.1 (13)</td>
<td>4.2 (20)</td>
</tr>
</tbody>
</table>

*Data from 1991 are Food 1 and Food 2 pooled; data from 1992 to 1995 are from Food 1 only.

<table>
<thead>
<tr>
<th></th>
<th>Adult females</th>
<th>Adult males</th>
<th>Juvenile females</th>
<th>Juvenile males</th>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Controls</td>
<td>Alive</td>
<td>4</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>P.Ex.</td>
<td>Alive</td>
<td>0</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Food 1</td>
<td>Alive</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>P.Ex. + Food</td>
<td>Alive</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Total (%)</strong></td>
<td>Alive</td>
<td>5 (100)</td>
<td>3 (75)</td>
<td>8 (89)</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
<td>0 (0)</td>
<td>1 (25)</td>
<td>1 (11)</td>
</tr>
</tbody>
</table>

Total overwinter survival = 85%; Monthly survival overwinter =97%

<table>
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<tr>
<th></th>
<th>Adult females</th>
<th>Adult males</th>
<th>Juvenile females</th>
<th>Juvenile males</th>
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<tr>
<td>Controls</td>
<td>Alive</td>
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<td>1</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>P.Ex.</td>
<td>Alive</td>
<td>0</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
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<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Food 1</td>
<td>Alive</td>
<td>7</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>P.Ex. + Food</td>
<td>Alive</td>
<td>7</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total (%)</strong></td>
<td>Alive</td>
<td>15 (94)</td>
<td>5 (83)</td>
<td>15 (88)</td>
</tr>
<tr>
<td></td>
<td>Dead</td>
<td>1 (6)</td>
<td>1 (17)</td>
<td>2 (12)</td>
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Total overwinter survival = 90%; Monthly survival overwinter =98%

ADULTS

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<tr>
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<tr>
<td></td>
<td>n</td>
<td>%</td>
<td>n</td>
<td>%</td>
<td>n</td>
<td>%</td>
</tr>
<tr>
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<td>50</td>
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<td>1</td>
<td>16.7</td>
</tr>
<tr>
<td>Red-Tail</td>
<td>-</td>
<td>-</td>
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<td>16.7</td>
</tr>
<tr>
<td>Lynx</td>
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<td>-</td>
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<td>Total mortalities</td>
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<td>7</td>
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JUVENILES

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<tr>
<td></td>
<td>n</td>
<td>%</td>
<td>n</td>
<td>%</td>
<td>n</td>
<td>%</td>
</tr>
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<td>7</td>
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<td>3</td>
<td>17.0</td>
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<td>6.7</td>
</tr>
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<td>9.5</td>
<td>1</td>
<td>5.5</td>
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<td>-</td>
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<td>Great Horned Owl</td>
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<td>20.0</td>
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<td>Total mortalities</td>
<td>21</td>
<td></td>
<td>18</td>
<td></td>
<td>15</td>
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</tbody>
</table>
APPENDIX IV. Adult arctic ground squirrel home ranges, 1993 to 1995.

TABLE 1. Average adult male and female home range sizes (± S.E.), and home range diameters, for all experimental treatments 1993 - 1995. Home ranges were calculated with program CALHOME (Kie et al. 1994) using the Minimum Convex polygon (MCP) method (Jennrich and Turner 1969) and excluded the outermost 5% of telemetry fixes obtained from each individual. Sample sizes are shown in brackets after each mean.

TABLE 2. Statistical comparisons of adult male and female home range sizes among years, and among treatments. Analysis of Variance was performed unless otherwise stated; data that did not meet the requirement of homoscedasticity were compared using a Welch’s ANOVA (Sokal and Rohlf 1995).

References


TABLE 1.

<table>
<thead>
<tr>
<th>TREATMENT</th>
<th>YEAR</th>
<th>AVERAGE ADULT FEMALE HOME RANGE SIZE (± S.E.) (Ha) (N)</th>
<th>FEMALE HOME RANGE DIAMETER (m)</th>
<th>AVERAGE ADULT MALE HOME RANGE SIZE (± S.E.) (Ha) (N)</th>
<th>MALE HOME RANGE DIAMETER (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>HOME RANGE DIA (m)</td>
<td></td>
<td>HOME RANGE DIA (m)</td>
<td></td>
</tr>
<tr>
<td>CONTROLS</td>
<td>1993</td>
<td>2.69±0.59 (12)</td>
<td>185</td>
<td>7.93±3.84 (6)</td>
<td>318</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>3.05±0.68 (13)</td>
<td>197</td>
<td>5.39±1.52 (6)</td>
<td>261</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>2.30±0.33 (23)</td>
<td>171</td>
<td>8.51±4.74 (3)</td>
<td>329</td>
</tr>
<tr>
<td>PREDATOR EXCLOSURE</td>
<td>1993</td>
<td>2.21±0.21 (14)</td>
<td>168</td>
<td>9.41±6.51 (3)</td>
<td>346</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>2.37±0.56 (15)</td>
<td>174</td>
<td>9.76±2.91 (5)</td>
<td>352</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>1.64±0.17 (17)</td>
<td>145</td>
<td>2.73±1.90 (2)</td>
<td>186</td>
</tr>
<tr>
<td>FOOD</td>
<td>1993</td>
<td>0.42±0.08 (18)</td>
<td>73</td>
<td>1.01±0.69 (3)</td>
<td>113</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>0.48±0.08 (12)</td>
<td>78</td>
<td>0.10±0.08 (2)</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>0.38±0.13 (16)</td>
<td>70</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PREDATOR EXCLOSURE +</td>
<td>1993</td>
<td>0.46±0.11 (12)</td>
<td>77</td>
<td>0.91±0.34 (10)</td>
<td>108</td>
</tr>
<tr>
<td>FOOD</td>
<td>1994</td>
<td>0.67±0.17 (16)</td>
<td>92</td>
<td>0.82±0.34 (5)</td>
<td>102</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>0.37±0.09 (20)</td>
<td>69</td>
<td>2.09 (1)</td>
<td>163</td>
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TABLE 2.

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<th>COMPARISON</th>
<th>SEX</th>
<th>F</th>
<th>DF</th>
<th>p</th>
</tr>
</thead>
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<td>CONTROLS (93-95)</td>
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<td>2</td>
<td>0.77</td>
</tr>
<tr>
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<td>FEMALE</td>
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<td>2</td>
<td>0.79</td>
</tr>
<tr>
<td>P.EX. (93-95)</td>
<td>MALE</td>
<td>1.00</td>
<td>2</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>FEMALE</td>
<td>0.87</td>
<td>2</td>
<td>0.42</td>
</tr>
<tr>
<td>FOOD (93-95)</td>
<td>MALE</td>
<td>(t-test)</td>
<td>3</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>FEMALE</td>
<td>3.49</td>
<td>2</td>
<td>0.03 (W)*</td>
</tr>
<tr>
<td>P.EX.+FOOD (93-95)</td>
<td>MALE</td>
<td>(t-test)</td>
<td>13</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>FEMALE</td>
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<td>2</td>
<td>0.64</td>
</tr>
<tr>
<td>AMONG TREATMENTS</td>
<td>MALE</td>
<td>12.86</td>
<td>3</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>FEMALE</td>
<td>47.47</td>
<td>3</td>
<td>&lt;0.0001 (W)</td>
</tr>
</tbody>
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*Welch’s ANOVA used for these comparisons because data were heteroscedastic.
APPENDIX V. Dates of earliest emergence of juvenile arctic ground squirrels on treatment and control areas, 1992 to 1995.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Controls</td>
<td>4 July</td>
<td>14 June</td>
<td>13 June</td>
<td>20 June</td>
</tr>
<tr>
<td>P.Ex.</td>
<td>≈5 July</td>
<td>18 June</td>
<td>13 June</td>
<td>≈20 June</td>
</tr>
<tr>
<td>Food</td>
<td>26 June</td>
<td>14 June</td>
<td>6 June</td>
<td>5 June</td>
</tr>
<tr>
<td>P.Ex.+Food</td>
<td>27 June</td>
<td>7 June</td>
<td>6 June</td>
<td>6 June</td>
</tr>
</tbody>
</table>
APPENDIX VI. Sex-specific dispersal of juvenile arctic ground squirrels in the boreal forest, 1993 to 1995.

Results of logistic regressions to determine which sex dispersed further, using distance as a continuous x-variable and the two sexes as discrete y-variables (u = unstable estimates). In all cases, there was one degree of freedom. P-values <0.05 mean that males dispersed significantly further than females on that particular treatment or in that particular year.
<table>
<thead>
<tr>
<th></th>
<th>Intercept estimate</th>
<th>Distance estimate</th>
<th>$r^2$</th>
<th>N</th>
<th>p</th>
<th>-LogLikelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>CONTROLS 93</td>
<td>u</td>
<td>u</td>
<td>1.00</td>
<td>8</td>
<td>&lt;0.00</td>
<td>4.50</td>
</tr>
<tr>
<td>CONTROLS 94</td>
<td>-3.80</td>
<td>0.03</td>
<td>0.55</td>
<td>12</td>
<td>0.17</td>
<td>4.21</td>
</tr>
<tr>
<td>CONTROLS 95</td>
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<td>0.01</td>
<td>0.32</td>
<td>16</td>
<td>0.11</td>
<td>3.46</td>
</tr>
<tr>
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<td>0.01</td>
<td>0.40</td>
<td>36</td>
<td>&lt;0.01</td>
<td>9.38</td>
</tr>
<tr>
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<td>0.009</td>
<td>0.45</td>
<td>17</td>
<td>&lt;0.03</td>
<td>5.31</td>
</tr>
<tr>
<td>P.EX. 94</td>
<td>u</td>
<td>u</td>
<td>1.00</td>
<td>15</td>
<td>&lt;0.00</td>
<td>9.55</td>
</tr>
<tr>
<td>P.EX. 95</td>
<td>-1.61</td>
<td>0.009</td>
<td>0.25</td>
<td>14</td>
<td>0.26</td>
<td>2.30</td>
</tr>
<tr>
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<td>0.01</td>
<td>0.42</td>
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<td>&lt;0.005</td>
<td>12.87</td>
</tr>
<tr>
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<td>-1.28</td>
<td>0.004</td>
<td>0.15</td>
<td>15</td>
<td>0.19</td>
<td>1.55</td>
</tr>
<tr>
<td>FOOD 94</td>
<td>-4.42</td>
<td>0.05</td>
<td>0.47</td>
<td>18</td>
<td>0.11</td>
<td>4.99</td>
</tr>
<tr>
<td>FOOD 95</td>
<td>-0.54</td>
<td>0.001</td>
<td>0.02</td>
<td>16</td>
<td>0.45</td>
<td>0.32</td>
</tr>
<tr>
<td>FOOD 93-95</td>
<td>-1.06</td>
<td>0.002</td>
<td>0.09</td>
<td>49</td>
<td>&lt;0.05</td>
<td>2.93</td>
</tr>
<tr>
<td>P.EX.+FOOD 93</td>
<td>-0.49</td>
<td>0.01</td>
<td>0.24</td>
<td>11</td>
<td>0.39</td>
<td>1.72</td>
</tr>
<tr>
<td>P.EX.+FOOD 94</td>
<td>u</td>
<td>u</td>
<td>1.00</td>
<td>15</td>
<td>&lt;0.00</td>
<td>10.10</td>
</tr>
<tr>
<td>P.EX.+FOOD 95</td>
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<td>0.001</td>
<td>0.05</td>
<td>15</td>
<td>0.34</td>
<td>0.55</td>
</tr>
<tr>
<td>P.EX.+FOOD 93-95</td>
<td>-0.41</td>
<td>0.001</td>
<td>0.07</td>
<td>41</td>
<td>0.14</td>
<td>1.98</td>
</tr>
<tr>
<td>1993 (all treatments)</td>
<td>-1.59</td>
<td>0.01</td>
<td>0.26</td>
<td>51</td>
<td>&lt;0.001</td>
<td>9.15</td>
</tr>
<tr>
<td>1994 (all treatments)</td>
<td>-4.43</td>
<td>0.03</td>
<td>0.67</td>
<td>60</td>
<td>&lt;0.003</td>
<td>25.54</td>
</tr>
<tr>
<td>1995 (all treatments)</td>
<td>-0.64</td>
<td>0.001</td>
<td>0.07</td>
<td>61</td>
<td>&lt;0.06</td>
<td>2.73</td>
</tr>
<tr>
<td>1993 to 1995 (treatments and years pooled)</td>
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<td>0.004</td>
<td>0.16</td>
<td>172</td>
<td>&lt;0.0001</td>
<td>18.98</td>
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</tbody>
</table>
APPENDIX VII. Results of Kruskal-Wallis rank-sum tests comparing dispersal distances for juvenile males and females among experimental treatments, 1993 to 1995.

<table>
<thead>
<tr>
<th>Year</th>
<th>Gender</th>
<th>$\chi^2$</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>Males</td>
<td>6.07</td>
<td>3</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>4.78</td>
<td>3</td>
<td>0.19</td>
</tr>
<tr>
<td>1994</td>
<td>Males</td>
<td>2.92</td>
<td>3</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>1.33</td>
<td>3</td>
<td>0.72</td>
</tr>
<tr>
<td>1995</td>
<td>Males</td>
<td>1.86</td>
<td>3</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>9.78</td>
<td>3</td>
<td>&lt;0.02</td>
</tr>
</tbody>
</table>
APPENDIX VIII. Dispersal and survival of juvenile arctic ground squirrels, 1993 to 1995.

Results of logistic regressions to determine whether juvenile mortality increases with increasing distance from the natal burrow, using distance as a continuous x-variable and survival to the end of the active season (0=dead; 1=alive) as discrete y-variables (u = unstable estimates). In all cases, there was one degree of freedom. P-values <0.05 mean that juveniles that dispersed longer distances from that particular treatment in that particular year were more likely to die.
<table>
<thead>
<tr>
<th></th>
<th>Intercept estimate</th>
<th>Distance estimate</th>
<th>r²</th>
<th>N</th>
<th>p</th>
<th>-LogLikelihood</th>
</tr>
</thead>
<tbody>
<tr>
<td>CONTROLS 93</td>
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<td>-0.04</td>
<td>0.24</td>
<td>6</td>
<td>0.50</td>
<td>0.65</td>
</tr>
<tr>
<td>CONTROLS 94</td>
<td>0.24</td>
<td>-0.004</td>
<td>0.11</td>
<td>12</td>
<td>0.34</td>
<td>0.89</td>
</tr>
<tr>
<td>CONTROLS 95</td>
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<td>-0.02</td>
<td>0.16</td>
<td>13</td>
<td>0.21</td>
<td>1.31</td>
</tr>
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<td>-0.01</td>
<td>0.09</td>
<td>31</td>
<td>0.29</td>
<td>1.77</td>
</tr>
<tr>
<td>P.EX. 93</td>
<td>-1.34</td>
<td>0.01</td>
<td>0.32</td>
<td>15</td>
<td>0.16</td>
<td>3.25</td>
</tr>
<tr>
<td>P.EX. 94</td>
<td>-1.87</td>
<td>0.002</td>
<td>0.06</td>
<td>15</td>
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<td>0.52</td>
</tr>
<tr>
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<td>u</td>
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<td>14</td>
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<td>3.60</td>
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<td>6.45</td>
</tr>
<tr>
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<td>0.002</td>
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<td>0.84</td>
<td>0.02</td>
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<td>17</td>
<td>0.72</td>
<td>0.10</td>
</tr>
<tr>
<td>FOOD 95</td>
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<td>0.002</td>
<td>0.13</td>
<td>14</td>
<td>0.18</td>
<td>1.13</td>
</tr>
<tr>
<td>FOOD 93-95</td>
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<td>0.001</td>
<td>0.03</td>
<td>44</td>
<td>0.22</td>
<td>0.78</td>
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<td>P.EX.+FOOD 93</td>
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<td>0.44</td>
<td>8</td>
<td>0.40</td>
<td>1.33</td>
</tr>
<tr>
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<td>u</td>
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<td>11</td>
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<td>0.61</td>
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<td>-1.60</td>
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<td>0.27</td>
<td>30</td>
<td>&lt;0.04</td>
<td>5.19</td>
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<tr>
<td>1993 (all treatments)</td>
<td>-1.00</td>
<td>0.002</td>
<td>0.08</td>
<td>43</td>
<td>&lt;0.09</td>
<td>2.27</td>
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<td>1994 (all treatments)</td>
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<tr>
<td>1995 (all treatments)</td>
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<td>52</td>
<td>&lt;0.02</td>
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<tr>
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<td>7.82</td>
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APPENDIX IX. Embryo scars of road-killed females.

Mean number of embryo scars (± S.E.) per female, based on a sample of squirrels road-killed on the Alaska Highway, 1993 to 1995. Sample sizes are shown in brackets after each mean.

<table>
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<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
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<td>Mean</td>
<td>5.0±0.36</td>
<td>6.33±0.33</td>
<td>5.57±1.13</td>
<td>5.35±0.39 (23)</td>
</tr>
<tr>
<td>Samples</td>
<td>(13)</td>
<td>(3)</td>
<td>(7)</td>
<td></td>
</tr>
</tbody>
</table>

Mode=5, median=5