REPRODUCTION, HIBERNATION, AND POPULATION REGULATION OF ARCTIC GROUND SQUIRRELS (*SPERMOPHILUS PARRYII PLESIUS*)

By

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ABSTRACT

Populations of arctic ground squirrels in the boreal forest of the southwest Yukon were studied in order to answer the following questions: (1) What are the mechanisms of population regulation in arctic ground squirrel populations (2) How does variation among individuals and their environment influence their reproduction and survival, and (3) How does variation in habitat influence hibernating strategies of arctic ground squirrels?

In spring 1996, control densities of ground squirrels were 1.6 per ha, and four other populations ranged in density from 3.2 to 30.1 per ha as a result of a 10-year (1987-96) large scale manipulation of food and predators in the boreal forest of the Kluane Boreal Forest Ecosystem Project. When the Kluane project terminated in spring 1996, I measured population densities, reproduction, emigration, and survival in all populations using live-trapping and radio-telemetry techniques until spring 1998.

Arctic ground squirrel populations were strongly regulated because all experimental populations declined to control densities within two years after the termination of the experimental manipulations. Two factors proved strongly density-dependent and hence were regulatory: (1) the proportion of females that weaned their litter and (2) overwinter survival. Simultaneous density-independent changes in weaning rate were also detected and were attributed to changes in the previous year's snow accumulation.

Female ground squirrels exhibited positive associations of life history traits. Squirrels in better condition at spring emergence were more likely to give birth, wean their litter, survive to the next breeding season, and reproduce once again. Nearly all females who failed during lactation did not survive to the next breeding season. The overwinter survival rate of females that successfully weaned a litter declined at a greater rate with increasing population density than did squirrels that never gave birth, indicating a cost to reproduction.

Ground squirrels hibernated distantly (24 m) from their summer burrows in relation to population density and in open or shrubby habitats that were likely to accumulate the most snow. Increased snow accumulation over hibernacula increased the minimum soil temperatures and decreased the rate of mass loss of hibernating squirrels suggesting a selective mechanism for the ability of ground squirrels to identify habitats that minimize their energy expenditure during hibernation.

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Chapter 1

INTRODUCTION

The prevalence of density dependence in natural populations and its role in population dynamics and life-histories of various species remains in question (Matos et al. 1999; McCullough 1999; Travis et al. 1999) after nearly seventy years since Nicholson's (1933) introduction of the term "control factor" (a.k.a. density-dependent factor) to the concept of population regulation. Although misuse of terminology is partially to blame for the extent of arguments about population regulation (Sinclair 1989), the prevalence of density independence in natural populations creates havoc in studies looking for density-dependent relationships. Density dependence may be nearly invisible in some environments where density independence is common, possibly suggesting that density dependence is irrelevant in regulating populations (Andrewartha and Birch 1954). In fact, density dependence may be expressed only periodically, but this does not weaken its importance in population regulation or in the evolution of life history traits of animals (McCullough 1999).

Advocates of density dependence in population regulation admit that density-independent factors have substantial effects in population dynamics. Caughley (1994) claims that environmental variation simply adds to the background variation in rates of increase in natural populations over long time scales. Sinclair and Pech (1996) even state that populations rarely, if ever, remain at their limit owing to occurrences of environmental stochasticity. Density dependence is a necessary condition of population regulation (Caughley and Sinclair 1994; Turchin 1999), but because of the occurrence of density-independent fluctuations in populations, it is not a sufficient condition of population regulation. Leirs et al. (1997) state that much of the controversy in population ecology is owing to the lack of integration of density-dependent and density-independent processes.

Models of density dependence and density independence (Sinclair 1989; Krebs 1994; Murray 1994) assume that all individuals in a population respond to densities with the same probability. Density-dependent mortality, for example, implies that the rate of mortality will be proportional to population density. Density-dependent models assume that all individuals have the same probability of dying, but clearly some individuals die and some do not, there is no intermediate rate of mortality for an individual unlike for reproduction where litter size can be reduced in proportion to population density. Why do changes in population density cause death of some and not others? How an organism responds to the density of conspecifics may depend on an array of factors such as social rank, age, condition, size, and experience. For example, in bighorn sheep (*Ovis canadensis*), Festa-Bianchet et al. (1998) found that heavier ewes were more likely to wean their young at high densities than lighter ewes. Furthermore they found that survival of ewes was density dependent but only for older ewes that did not give birth. For the other ages and reproductive classes, survival was density independent. Such complex interactions among individual states with population density illustrate the importance of considering individual variation in life-history theory and population regulation.

Population dynamics of arctic ground squirrels in the boreal forest

Arctic ground squirrels are distributed throughout the mainland arctic tundra and northern boreal forests of Canada and Alaska (Howell 1938; Banfield 1974; Nadler and Hoffmann 1977). In alpine and arctic tundra habitats, populations are suggested to be stable and limited by food, burrow availability, and spacing behaviour (Carl 1971; Green 1977; Batzli and Sobaski 1980). Carl (1971) assumed that predators did not limit populations, but only removed the surplus of squirrels that would otherwise be forced to disperse from the best quality habitats. However, patterns of population dynamics are inconclusive because all studies on arctic populations of arctic ground squirrels have been short term (≤ 2 years) and primarily qualitative. In the boreal forest habitat of the southwest Yukon, arctic ground squirrel numbers fluctuate 3-fold in close synchrony with the 10-year cycle of snowshoe hare (*Lepus americanus*) populations (Boutin et al. 1995). Here, arctic ground squirrels exist at relatively low densities (0.7-2.2 per ha) (Boutin et al. 1995) compared with open meadow habitats (13-16 per ha, Lacey et al. 1997), alpine tundra (6.6 per ha, Green 1977), and arctic tundra (5.5 per ha, Carl 1971).

Experimental manipulations of food and predators by the Kluane Boreal Forest Ecosystem Project (1987 - 1996) (Krebs et al. 1995) showed that arctic ground squirrel populations in the boreal forest are limited by a complex interaction between food availability and predators (Hubbs and Boonstra 1997; Byrom et al. 2000; Karels et al. 2000). In comparison with unmanipulated populations of ground squirrels the experimental treatments had the following effects. In the absence of mammalian predators, ground squirrels were in better condition, had greater reproductive rates, and doubled in population density. In the presence of food supplementation, ground squirrels were in better condition, had greater and earlier reproduction, and reached 4- to 7-fold densities. In the absence of mammalian predators and in the presence of food supplementation ground squirrels showed all the previous effects but to a greater degree than that of the single factor manipulations of food and predators such that populations reached 19-fold that of control populations. Immigration (Hubbs and Boonstra 1997), emigration (Byrom and Krebs 1999), juvenile growth rates (Hubbs and Boonstra 1997; Karels et al. 2000), summer survival (Byrom et al. 2000), overwinter survival (Hubbs and Boonstra 1997; Karels et al. 2000) were not influenced by the experimental manipulations of food and predators.

The direct impact of predators on ground squirrels by predation was most evident during the decline of hare populations when hares became scarce and predator numbers were high (1990 - 1992) (Boutin et al. 1995). During this period, predation rates on ground squirrels were high (32 - 49%) and ground squirrel populations on controls declined (48 to 56% Hubbs and Boonstra 1997). However, when predators became scarce, predation rates on controls were lower (3 - 30% Byrom et al. 2000) and populations increased 3-fold from 1993 to 1996 (Karels et al. 2000). However, predators had a noticeable indirect effect on populations during 1993 - 1996 when weaning rates of adult female squirrels were 17 to 37% greater in the absence of mammalian predators compared with squirrels on controls (Karels et al. 2000). Unfortunately, this effect was not measured by Hubbs and Boonstra (1997) so it is unknown if the sublethal effect of predators on ground squirrel reproduction was more intense from 1990 - 1992 when predators were abundant. However, among the experimental treatments, survival rates were similar during the decline and thus direct predation could not account for the differences in population density observed by Hubbs and Boonstra (1997). This suggests that strong sublethal effects of predators on ground squirrels were also important during the decline.

The experimental manipulations of the Kluane Boreal Forest Ecosystem Project and the temporal changes in predator abundance induced by the snowshoe hare cycle clearly demonstrated population limitation but not regulation. Only when per capita rates of production and mortality are density dependent can regulation be concluded (Sinclair and Pech 1996). Initially, the experiments were not designed to test for density dependence and thus regulating factors were not discernable from limiting factors, but at its completion in 1996 the Kluane Project had set up a powerful experimental design to test the role of density dependence in population regulation and life history—the central focus of this thesis.

Thesis questions and layout

The research presented in this thesis focussed on three main questions: (1) What are the mechanisms of population regulation in arctic ground squirrel populations; (2) How does variation among individuals and their environment influence their reproduction and survival; and (3) How does variation in habitat influence hibernating strategies of arctic ground squirrels? The central experimental design is built upon a range of ground squirrels densities (1.6 - 30.1 per ha) that remained at the termination of the Kluane Boreal Forest Ecosystem Project (1987 - 1996) (Krebs et al. 1995) in spring 1996. These populations served as a density-manipulation experiment (Cappuccino 1995; Harrison and Cappuccino 1995; Cappuccino and Harrison 1996) in which to test hypotheses of the role of population density on reproduction, survival, and rate of population change and how population density interacts with other factors that influence individual reproductive and survival strategies.

In Chapter 2, I describe the density manipulation experiment and test for population regulation by analysing rates of reproduction (birth, litter size, weaning) and survival (summer and winter) for density dependence. I then present the mechanisms of population regulation of arctic ground squirrels by showing which factors contribute to the convergence of experimental populations with controls—the ultimate criteria for detecting population regulation (Murdoch 1970).

In Chapter 3, I examine the reproductive and survival strategies of adult female ground squirrels under increasing intraspecific competition for limited resources. Using the density manipulation experiment, I test how population density interacts with variation in condition and age among individual squirrels to influence birth and weaning rates. I then tested how the above parameters including the reproductive state—having weaned a litter, having lost a litter during lactation, or not having giving birth—influence summer and overwinter survival.

In Chapter 4, I test the hypothesis that ground squirrels maximize their overwinter survival by selecting hibernacula in habitats that minimize their overwinter energy expenditure. This part of the study was conducted when the Kluane experimental manipulations were in progress and thus tests the impact of population density, food, and the presence of predators on the selection of hibernacula.

Chapter 5 summarizes the main the conclusions of this research and presents recommendations for future research.

Chapter 2

POPULATION REGULATION OF ARCTIC GROUND SQUIRRELS

Introduction

The topic of population regulation has a history of heated debates that continue to this day (Murray 1999; Turchin 1999). The initial debates focused on the role of biotic factors (Howard and Fiske 1911) versus abiotic factors (Uvarov 1931) in controlling population densities. However, since Nicholson's (1933) theory that populations can only be regulated by factors that act in a density-dependent manner, ecologists have focused the debate on questions of the relative importance of density-dependent versus density-independent processes (Andrewartha and Birch 1954). In particular, is density-dependent regulation necessary to explain persistence of populations (Andrewartha and Birch 1954; Murdoch 1994; Sinclair and Pech 1996) and what is its strength or frequency in natural populations (Strong 1984; Wolda 1995)? Neither process needs to be exclusive, since population size could be determined by interactions between density-dependent and density-independent processes (Chitty 1967). However, clear demonstration of both processes affecting population demography and dynamics are rare (Leirs et al. 1997).

Arguments in population regulation have been aggravated by misuse of terminology. Sinclair (1989) addressed this problem and stated that a more rigorous attention to definition was needed in the future to avoid confusion of meaning in the literature. I begin with Murdoch and Walde's (1989) definition that density dependence is "a dependence of per capita population growth rate on present and/or past population densities". Although this is a clear definition and is currently used in the literature (Holyoak 1994; Turchin 1995), it implies that density is the mechanism driving population change. However, density per se is still a black box that gives little or no understanding of the precise processes involved. This is why it is criticized by those who approach the problem of population regulation using a mechanistic approach (Krebs 1995). Whereas followers of the density-dependent paradigm seek density-dependent factors—the causes of processes that relate to population density [e.g. predation or competition (Sinclair 1989)]—followers of the mechanistic paradigm seek how rates of change in birth or death are affected by changes in the factor of interest (Krebs 1995). These two approaches ask two different questions. The density dependence approach is more concerned with population persistence. It asks "what processes allow a species' population to persist without increasing to infinity or declining to extinction?". The mechanistic approach asks "what factors are the causes of fluctuations in population density?".

Both paradigms attempt to explain limitation and regulation. Population limitation refers to all processes that set equilibrium density (Sinclair 1989; Sinclair and Pech 1996) where loss from the population is balanced by gain. Any factor that changes loss or gain is a limiting factor (Sinclair 1989). Population regulation refers to all processes that return a population to its equilibrium density (Nicholson 1933; Murdoch 1970) and are density dependent (Sinclair 1989; Sinclair and Pech 1996). Whereas the strength of the density dependence paradigm is in detecting regulation, the strength of the mechanistic paradigm is in detecting limitation. The benefit of manipulative experiments is recognized by both paradigms (Sinclair 1989; Krebs 1991) so it becomes clear that in order to fully understand population dynamics we must employ both approaches using manipulative experimental designs.

Density-perturbation studies offer the strongest approach to detecting regulation and identifying its mechanisms (Murdoch 1970; Sinclair 1989; Caughley and Sinclair 1994; Harrison and Cappuccino 1995; Cappuccino and Harrison 1996). There are two alternatives to this approach: the convergence experiment and the density-manipulation experiment. The convergence experiment (Murdoch 1970) first perturbs densities from their equilibrium and concludes that the population is regulated if it returns to pre-disturbance densities. This experiment allows one to measure population processes and determine the mechanisms and their strengths as they re-establish the population towards an equilibrium density. There are two main disadvantages of this approach. First, it may take many generations to reach equilibrium before regulation can be concluded. Second, density-independent factors such as environmental fluctuations can vary the rate of convergence even though regulating mechanisms are operating (Turchin 1990). Alone, this approach is insufficient. The density-manipulation experiment produces contrasting population densities by removal or addition of individuals. Thus, population processes can be simultaneously monitored at different densities and a determination made of which processes are influenced by density (Harrison and Cappuccino 1995). The advantage of this approach is that it needs only one generation to detect direct density dependence (Cappuccino and Harrison 1996). If conducted with multiple populations of varying densities over a sufficient period of time, the density-manipulation experiment can provide a rigorous test of regulation and distinguish between the many forms that regulating factors can take (e.g. delayed density dependence) (Cappuccino and Harrison 1996). I used the density-manipulation experiment to elucidate the mechanisms regulating arctic ground squirrel (*Spermophilus parryii plesius*) populations living in the northern boreal forest.

Arctic ground squirrels are distributed throughout the mainland arctic tundra and northern boreal forests of Canada and Alaska (Howell 1938; Banfield 1974; Nadler and Hoffmann 1977). Populations of arctic ground squirrels in alpine and arctic tundra habitats are suggested to be stable and limited by food, burrow availability, and spacing behaviour (Carl 1971; Green 1977; Batzli and Sobaski 1980). In arctic environments, populations were assumed not to be limited by predators. Carl (1971) regarded the role of predators as only removing the surplus of squirrels that would otherwise be forced to disperse from the best quality habitats. However, population dynamics could not be conclusively determined because all studies on arctic populations of arctic ground squirrels were short term (≤ 2 years). In the boreal forest habitat of the southwest Yukon, arctic ground squirrels exist at relatively low densities (0.7-2.2 per ha) (Boutin et al. 1995) in contrast to open meadow habitats (13-16 per ha, Lacey et al. 1997), alpine tundra habitats (6.6 per ha, Green 1977), or arctic tundra habitats (5.5 per ha, Carl 1971). Furthermore, boreal forest populations fluctuate 3-fold in close synchrony with the 10-yr cycle of snowshoe hare (*Lepus americanus*) populations (Boutin et al. 1995).

As part of the Kluane Boreal Forest Ecosystem Project (Krebs et al. 1992; Krebs et al. 1995), manipulations of both food and predators over a 10-yr period (1987-1996) (Hubbs and Boonstra 1997; Byrom et al. 2000; Karels et al. 2000) resulted in the conclusion that arctic ground squirrels are limited by an interaction between predators and food acting primarily through changes in reproduction (Karels et al. 2000). These studies were able to examine the limiting roles of food and predators but were unable to determine which factor(s) operated in a density-dependent manner. At the completion of the Kluane Boreal Forest Ecosystem Project, four of these experimental manipulations resulted in ground squirrel populations that ranged from 2 to 19 times the density found in control populations (Karels et al. 2000). Thus, this was an ideal situation to examine population regulation and to observe and distinguish among processes that return these populations to equilibrium densities.

Life history

After an 8-9 month hibernation period (Hock 1960), arctic ground squirrels emerge from hibernacula in early to late April, with males emerging first and followed 7-10 days later by females (McLean and Towns 1981; Lacey et al. 1997; Buck and Barnes 1999a). At emergence, females represent 76% of the population (Karels, unpublished data) and both yearling and adult females are sexually receptive three to four days after emerging (Lacey et al. 1997). Breeding can extend into early May owing to the variation in emergence dates (Lacey 1991). Young are born in mid- to late May following a 25-day gestation and appear above ground close to weaning in mid- to late June, 25 days after birth (Mayer and Roche 1954; Lacey et al. 1997). Dispersal of juveniles occurs in July and is extremely male biased (Lacey 1991). In our study area, Byrom and Krebs (1999) found that rates of natal philopatry were 88% for females and 28% for males. She found that males dispersed long distances (515 ± 107 m) compared with females (120 ± 28 m) and that dispersal was independent of food resources and population density with exception that females showed increased dispersal only at exceptionally high densities

(23 per ha, 16-fold that of control populations). Squirrels begin hibernation in sequence: adult females enter first (late July to early August), followed by juvenile females (late August and throughout September), and then followed by males (August into October) (McLean and Towns 1981).

Study Site and Methods

Study site

My study was located along the Alaska Highway within the Shakwak Trench east of Kluane Lake in the southwest Yukon Territory, Canada (61°N, 138°W). There are four major vegetation types in this valley: white spruce forests (*Picea glauca*) cover 50% of the area and have an understory of willow (*Salix* spp.) and birch (*Betula glandulosa*); shrub meadows of willow and birch cover 33%; and grass meadows cover 7% (Boutin et al. 1995); trembling aspen (*Populus tremuloides)* stands (10%) are distributed among the three other vegetation types (C. J. Krebs pers. comm.).

The Kluane Lake area experiences a mean annual temperature of -3.9 ± 0.2 °C and receives an average of 284 ± 10 mm total annual precipitation (data from Burwash Landing Climatological Station 1967-1995). The climate is classified as cold continental and snow cover exists from October to early May (Boutin et al. 1995).

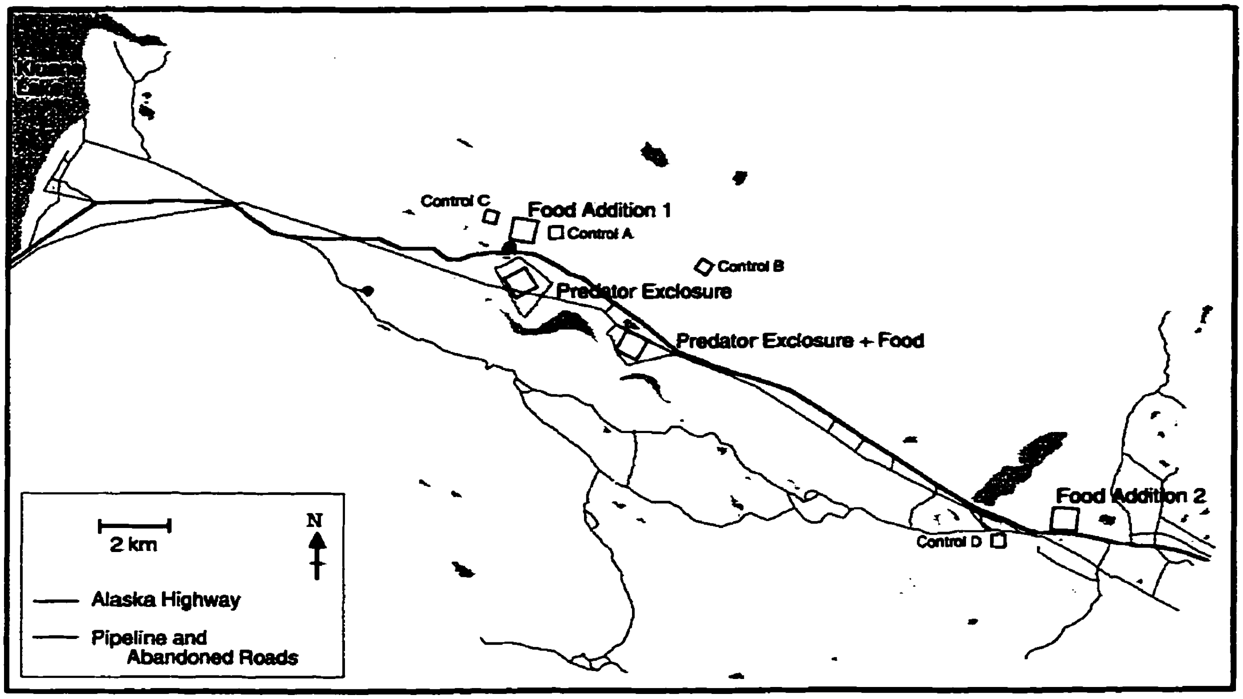


Figure 2.1 Location of experimental sites and controls of the Kluane Boreal Forest Ecosystem Project along the Alaska Highway in the south-west Yukon Territory, Canada. Experimental manipulations ceased in spring 1996.

Experimental Design

I monitored four 8 to 10-ha control areas (labeled Controls A through D) (Figure 2.1) that I assumed to be near equilibrium densities of 1.6 ± 0.15 squirrels per ha in spring. In addition, I monitored populations within four areas that were previously manipulated as part of the Kluane Boreal Forest Ecosystem Project. I present these areas in order of least to greatest population density describing the manipulations that produced the final ground squirrel density as of spring 1996 when my study began.

1. Predator Exclosure: From 1987 to spring 1996, a 1-km^2 area was enclosed within a 2.2-m high 8600 V electric fence in 1987 to keep out large mammalian predators (lynx [*Lynx canadensis*] and coyotes [*Canis latrans*]). A 10-ha portion of the 36-ha hare trapping grid was covered with a barrier of nylon monofilament (2 m above ground spaced 20 cm apart) to exclude avian predators. A 9-ha ground squirrel trapping grid was located under the monofilament. This manipulation produced ground squirrel densities twice that of controls (3.3 per ha) and is henceforth referred to as the post-predator exclosure when describing post-manipulation effects.
2. Food Addition: From 1988 to winter 1995, *ad libitum* supplemental food (commercial rabbit chow; 16% protein; Shur-Gain, Maple Leaf Foods Inc., Edmonton, Alberta) was added to two 36 ha areas (Food 1 and Food 2) at a rate of approximately 300 kg (8.3 kg per ha) every 5-6 days throughout the entire year. Squirrels were trapped within 8-ha areas of each treatment. Food addition 1 produced ground squirrel densities 7.2-fold (11.6 per ha) that of controls and henceforth is referred to as post-food 1. Food

addition 2 produced ground squirrel densities 3.7-fold (5.9 per ha) that of controls and henceforth is referred to as post-food 2.

3. Predator Exclosure + Food Addition: From 1988 to spring 1996 the above two treatments were combined on another 1-km^2 area using the same protocols as already described. A monofilament barrier was not erected and thus this treatment only excluded mammalian predators. Squirrels were trapped within an 8-ha area of this treatment. This manipulation produced ground squirrels densities 19-fold (30.1 per ha) that of controls and henceforth is referred to as post-predator exclosure + food.

Within this 1-km^2 site, two 2.5-ha areas, 270 m apart and 270 m from the original squirrel trapping area, were selected to continue the food supplementation program to maintain the effects of food addition after the main infrastructure was dismantled. I will refer to these sites as Food Addition A and Food Addition B. Although these areas had never been trapped for ground squirrels, densities were similar to that of the original trapping area (30.8 and 28.4 per ha) in spring of 1996 regardless of their small size in relation to the original 8-ha trapping area thus demonstrating that edge effects were negligible. Beginning in 1996, food was distributed from late April to early September at a rate of 20 kg per ha per week, more than double that of previous years. I stockpiled chow (40 kg per ha) during the last week of the field season in early September to provide food to the few remaining squirrels that had not entered hibernation. Both Food Addition A and Food Addition B were fed in 1996. However, Food Addition B was not fed in 1997 in order to create an additional density-manipulation experimental site at high density (11.2 per ha in 1997) to monitor population processes as ground squirrel populations converged to equilibrium density.

Demography and density measurements

A regular schedule of live trapping started in late April to early May of each year (1996-1998) and ended in late August in all years to monitor survival, reproductive status, and mass. More frequent trapping occurred during the emergence of juveniles (young-of-the-year) from their natal chambers in mid-June. Squirrels were captured using Tomahawk live traps (14 × 14 × 40 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with peanut butter. Traps were placed at burrow sites to increase recaptures of individuals. Two or three traps were placed at burrow systems that had ≥ 3 burrow openings. Traps were set at 0800 and were checked twice at 1-1.5-h intervals. Each squirrel was removed from the trap into a netted bag and marked in each ear with uniquely numbered metal eartags. At each capture I recorded eartag number, sex, weight, zygomatic arch breadth, and reproductive status. Females were recorded as lactating (nipples large and secreting milk) or not lactating (nipples small or dried).

I conducted a complete population census twice each year to accurately estimate population sizes. The first census provided overwinter survival and spring density estimates and occurred in a 2-3 week period starting the second week of May, whereas the second census provided post-reproduction and pre-hibernation densities and occurred from mid-July into the first week of August. During a census, populations were trapped for 3 to 4 consecutive days three times per day beginning at 0700 at 1.5-h intervals. Before analysing, records were pooled for each day separately to reduce hourly variation in trappability among individuals. Population estimates and standard errors of the estimate were calculated using a closed population mark-recapture heterogeneity model (jackknife) (Pollock et al. 1990) from program CAPTURE (Otis et al. 1978) as recommended by Menkens and Anderson (1988) and Boulanger and Krebs (1994). Fall densities for Food Addition A and Food Addition B in 1996 and 1997 were estimated as the minimum number alive because trapping could not be conducted over three consecutive days owing to interference by grizzly bears.

I fitted radio-collars (Model PD-2C, Holohil Systems Ltd., Carp, Ontario, Canada) on adult females shortly after spring emergence from hibernation to monitor fates of disappearing individuals during summer and to aid in location of natal burrows.

Overwinter survival was calculated from trapping records as the proportion of individuals captured in the spring that were present in the population prior to hibernation in the previous year (late July – September). Owing to male biased dispersal patterns and small sample sizes for males, I limited my analysis of overwinter survival to adult and juvenile females.

To determine weaning success and litter size I needed to locate natal burrows. Burrow sites belonging to radio-collared females were located at night during the first week of June, just prior to the first emergence of juveniles. Within a week of the first sign of juvenile emergence, intensive trapping occurred at these burrows using as many as 10 traps per burrow site in order to capture all of the juveniles born to that female. Juveniles typically remain close to the natal burrow for the first week (Lacey 1991). However, some mothers move their young immediately upon emergence to their adjacent burrow system (McLean 1981). In some cases, adult females share burrow systems or live in close proximity and mixing of juveniles among litters can occur even before emergence (Lacey et al. 1997). When this occurred, all juveniles from the mixed litters were captured. Litter sizes for each treatment were estimated by dividing the total number of juveniles caught at these targeted burrow systems by the total number of breeding females that lived within the targeted burrow systems. Hence, I did not assign a measurement of error to the estimate because I could not measure each litter separately. The weaning rate of the population was calculated as the proportion of females (lactating and not lactating) that had litters that appeared above ground.

Environmental conditions

Weather data collected at the Burwash Landing Climatological Station, which is located approximately 60 km from our study site, was used as an approximate measure of weather conditions in our study area to compare relative weather patterns among years. In addition, the initiation of the growing season was estimated from the appearance of foliage on a large stand of aspen trees (*Populus tremuloides*) in my study area. Millar (1972) used aspen growth as an indicator of the growing season in his study in southwest Alberta and noted that the appearance of fresh growth in other plant species was closely synchronized with that of the aspen. In my study area, this appeared to be true as well, as many species such as willow, birch, and various herbs, appeared to produce new growth within one week of appearance of aspen leaves.

Herbivore impacts on vegetation

To determine if intensity of herbivory on natural vegetation varied with density of ground squirrel populations, I measured the standing-crop dry weight biomass of herbs and grasses in mid- to late July in both 1996 and 1997. I measured only those species that are present in the diet of arctic ground squirrels according to studies done in our area (Lincoln 1972; McLean 1985). These were: lupines (*Lupinus arcticus*), yarrow (*Achillea* *borealis*), legumes (*Hedysarum* sp., *Oxytropis* sp., and *Astragalus* sp.), goldenrod (*Solidago* sp.), fireweed (*Epilobium angustifolium*), bluebell (*Mertensia paniculata*), pussy toes (*Antennaria* sp.), and fescue grass (*Festuca altacia*). Plants were sampled from 30 stations within each of the post-experimental sites and controls A and D. Stations were arranged at 30-m intervals along three parallel 270-m long transects with 90 m separating the transects. Each station consisted of two adjacent 0.25-m^2 areas, one a control and the other an exclosure of 2.54-cm wire mesh (1 m tall). Exclosures were constructed in early May of each year before emergence of vegetation. The mesh was small enough to exclude squirrels and hares but not mice, voles, or insect herbivores. Within a 0.09-m^2 quadrat centered within each 0.25-m^2 area, plants were identified, clipped at ground surface, oven-dried, and weighed separately. Although 30 stations were constructed on the Food Addition A, only 14 and 15 were sampled in 1996 and 1997 respectively, owing to damage and interference from grizzly bears.

Statistical Analysis

All statistical tests were performed according to procedures in Zar (1984) and Sokal and Rohlf (1995). Prior to analyses, all continuous variables were tested for the assumptions of parametric statistics using an *F*-test for equality of variances, and Kolmogorov-Smirnov goodness of fit test for normality. All proportional data were arcsine transformed as recommended by Krebs (1999) and density values were log-transformed prior to regression. Prior to ANOVA, plant biomass data were transformed by a Box-Cox transformation procedure ($\lambda = 11.4$) implemented with program Ecological Methodology (Krebs 1998). All analyses were performed using Program Statview (SAS Institute Inc. 1998), except for ANCOVA which was performed using Program

SuperAnova (Gagnon et al. 1991). All means are expressed with ± 1 standard error unless otherwise indicated.

Results

Population change

Population densities of arctic ground squirrels (± 1 SE of the estimate) on experimental sites and controls are shown in Figure 2.2. All experimental sites attained maximum spring densities in 1996 after 10 years of supplemental food and/or predator exclusion (Karels et al. 2000). After these manipulations ceased, these same populations declined in a density dependent manner (Figure 2.3) ($r^2 = 0.91$, $n = 9$, $P < 0.001$) such that by spring 1998, densities were similar to controls (Figure 2.2). Continued food supplementation on 2.5-ha segments of the predator exclosure + food treatment (Food Addition A and B) did not prevent a population decline (Figure 2.2). However the rate of decline was slowed (Figure 2.2 and Figure 2.3) such that densities were still 1.9 times those on the post-predator exclosure + food and 2.9 times those on controls.

Reproduction

I used presence of lactation as indication that a female ground squirrel had given birth. The proportion of females lactating was negatively related to population density in

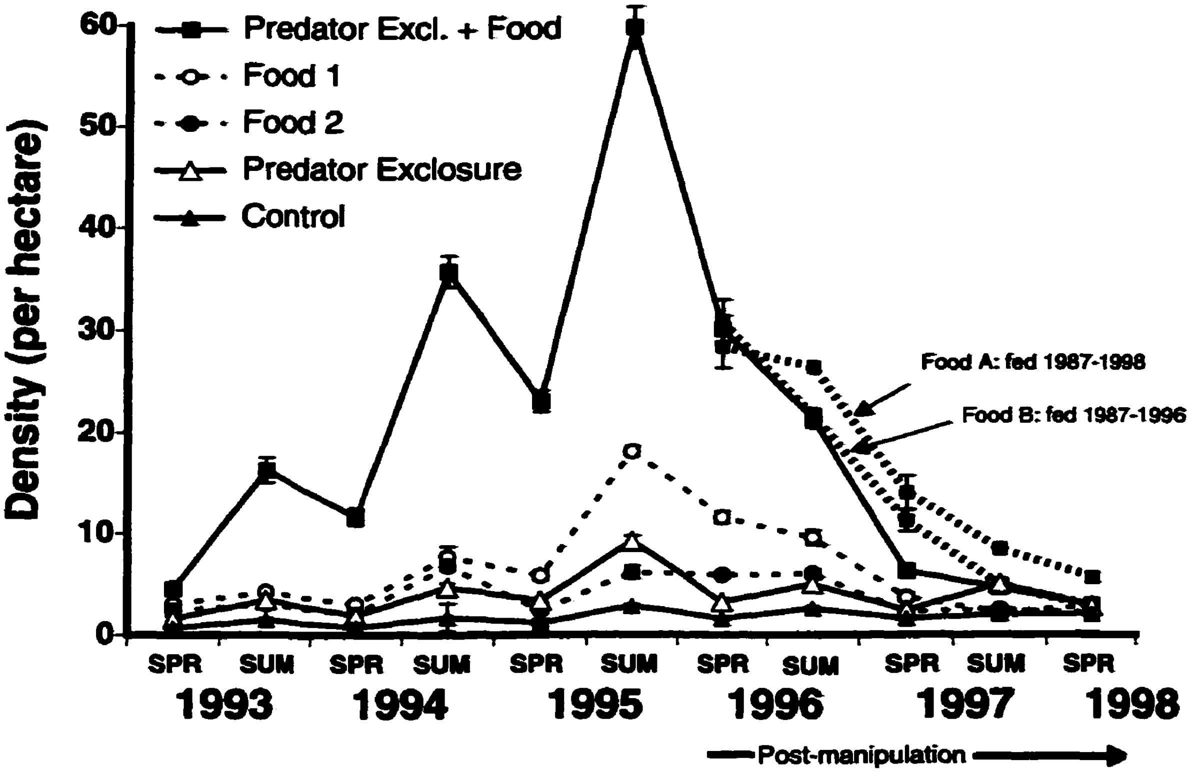


Figure 2.2 Population densities of arctic ground squirrels in the southwest Yukon Territory. The legend refers to the experimental treatments of the Kluane Boreal Forest Ecosystem Project. Data from 1993 to 1995 are from Karels et al. (2000). Food addition was terminated and predator exclosures removed by spring 1996. Two 2.5-ha areas (Food A and B) within the Predator Exclosure + Food treatment were food supplemented throughout 1996. One of the 2.5-ha areas (Food A) was also fed through to 1998.

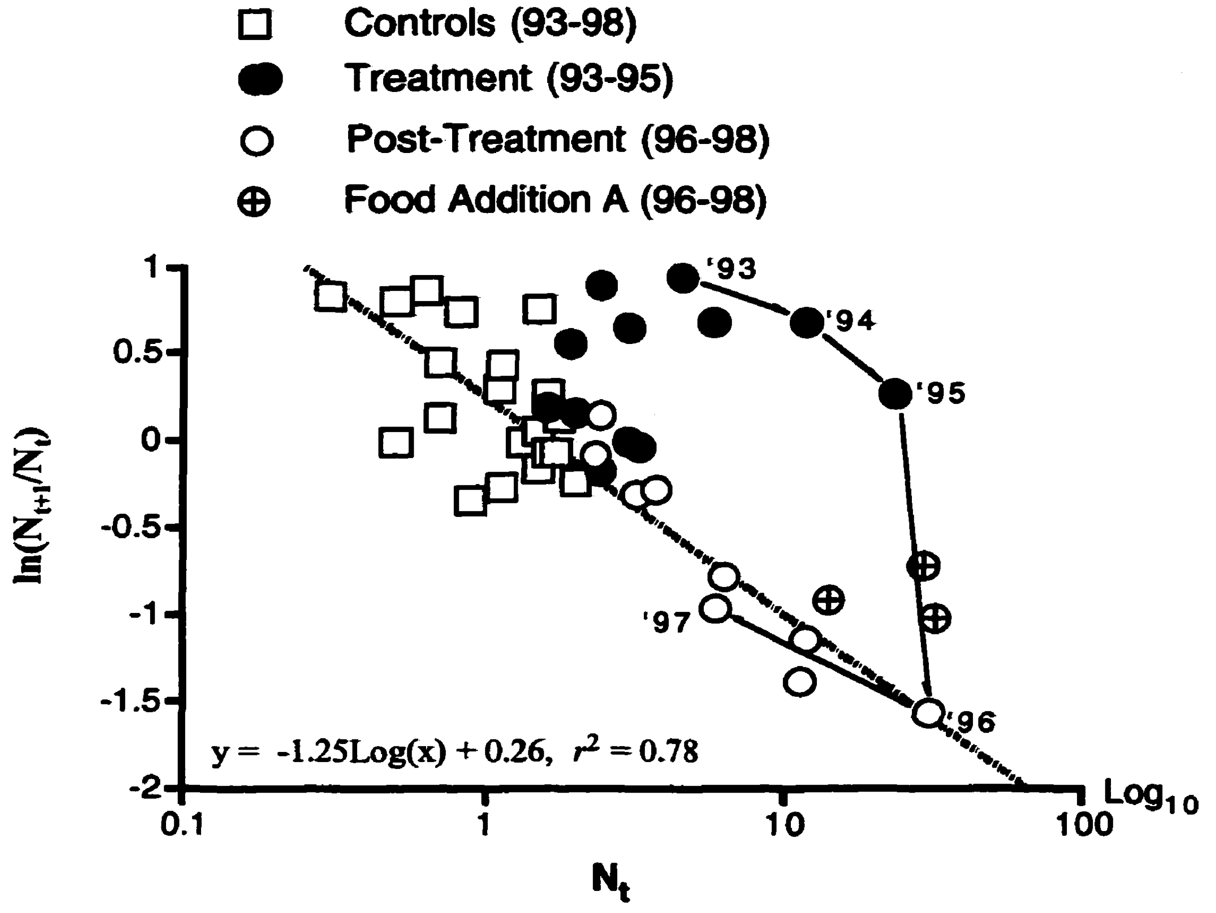


Figure 2.3 Regression curve showing density-dependent annual rates of increase (N_{t+1}/N_t) for spring breeding populations of arctic ground squirrels on controls (1993-1998) and on experimental sites after treatments were removed (1996-1998). Values of $\ln(N_{t+1}/N_t) > 0$ or < 0 indicate population growth and decline respectively. Rate = 0 indicates stable population density. Only population densities from 1993 onwards are presented because pre-1993 populations were declining as a function of predator abundance (Hubbs and Boonstra 1997). On experimental treatments prior to 1996, populations show positive growth. When manipulations ceased, populations showed negative growth and strong density dependence. The arrows on the figure illustrate the sequence of rates of increase on the predator exclosure + food site beginning with '93, the growth from 1993 to 1994.

both years (Table 2.1). However lactation rate was ≥ 68% on all sites except those on the two high density sites which had low lactation rates (post-predator exclosure + food 1996: 40% and post-food addition B 1997: 9%) (Figure 2.4). When these sites were removed from the analyses, then for 4 of 5 sites in 1996 and 5 of 6 sites in 1997 the proportion of females lactating declined only slightly and non-significantly with population density (1996: $r^2 = 0.42$, $n = 4$, $P = 0.35$; 1997: $r^2 = 0.09$, $n = 5$, $P = 0.62$). Food addition on the 2.5-ha segments of the former predator exclosure (Food Addition A and B) maintained high rates of lactation in female squirrels despite the high densities. Therefore lactation appeared to be strongly limited by food but only at very high densities.

Reproduction, as measured by the proportion of adult female squirrels weaning a litter, was strongly and negatively density dependent in both 1996 and 1997 (Table 2.1, Figure 2.5). The strength of density-dependence, that is, the rate of change in weaning as a function of density, was similar in both years (one-way ANCOVA: year × density, $F = 0.17$, $df = 1$, $P = 0.90$). Despite lower densities in 1997 on the experimental sites, the proportion of females weaning litters dropped by nearly 30% from 1996 to 1997 when corrected for density (one-way ANCOVA, $F = 57$, $df = 1$, $P < 0.001$).

Populations that were food supplemented (1996: $n = 2$; 1997: $n = 1$) were significant outliers from the regression each year (Dixon's test: for 1996, $P < 0.01$ for both populations; for 1997 $P = 0.01$). Thus, at the same density, supplemental food significantly increased the proportion weaning litters (1996 = 0.89, $n = 2$; 1997 = 0.82, $n = 1$). However, despite a decline in density from 1996 to 1997 (55%), the population that was continually fed through 1997 (Food Addition A) showed a slight decline in weaning rate (7%), consistent with, but not to the same degree, as the decline in weaning rate in all other populations.

Estimates of litter size were derived from only those litters that appeared above ground (i.e. emerged litter size ≥ 1). Therefore some sites where all litters failed were not included in the estimate. Litter size did not vary in relation to population density (Table 2.1, Figure 2.6). Food addition did not increase litter size when densities were high in 1996 but did increase litter size when densities were lower in 1997.

Survival

Summer survival of adult females was not significantly related to population density in either year (Table 2.1, Figure 2.7). In contrast, overwinter survival was strongly and negatively related to population density (Table 2.1, Figure 2.8). There was no difference in the strength of density dependence between years (one-way ANCOVA: year × density, $F = 0.251$, df = 1, $P = 0.63$) nor was there any difference in survival between years when the effects of density were removed (one-way ANCOVA: $F = 0.032$, df = 1, $P = 0.86$). Food supplementation improved overwinter survival (0.47-0.58) but only relative to non-supplemented high-density areas (0.11 – 0.20) (Figure 2.8). The proportion of survivors on food supplemented populations (1996: n = 2; 1997: n = 1) were statistically significant outliers from the regressions of remaining populations (Dixon's test: for 1996, $P < 0.05$ for both populations; for 1997 $P < 0.05$). However, food addition did not completely compensate for the effects of population density

Table 2.1 Linear regression statistics of variables tested for density dependence where x = log(density). All proportional data were arcsine transformed. Level of significance is $\alpha = 0.005$ when adjusted by Bonferroni method for multiple tests of significance. Sample sizes are given of the number of squirrels on each site that were used to calculate each variable.

Variable	**Linear Regression**					**Sample size of squirrels per site***						
	Year	Equation	r^2	N	*P*	C	P-PE	P-F1	P-F2	P-PE+F	+FA	+FB[†]
Lactating	1996	$-0.32x + 1.25$	0.70	5	0.076	22	24	44	25	80	47	39
	1997	$-0.88x + 1.50$	0.55	6	0.092	16	16	17	9	28	16	11
Weaning	1996	$-0.94x + 1.48$	0.97	5	< 0.003	10	9	9	7	15	9	9
	1997	$-1.11x + 1.16$	0.89	6	< 0.005	9	9	9	7	16	6	10
Litter Size	1996	$-0.38x + 2.89$	0.19	4	0.57	9	13	6	6	0	28	15
	1997	$-1.57x + 3.21$	0.11	4	0.68	6	7	4	4	0	5	0
Summer Survival	1996	$0.07x + 1.11$	0.01	5	0.87	10	9	11	11	15	11	12
	1997	$0.49x + 0.88$	0.06	5	0.70	10	8	8	10	8	7	0
Overwinter Survival	1996	$-0.95x + 1.54$	0.88	5	0.019	21	34	53	31	131	32	36
	1997	$-1.08x + 1.08$	0.91	6	< 0.004	19	22	12	7	25	9	8

*sites are abbreviated as follows: control (C), post-predator exclosure (P-PE), post-food 1 (P-F1), post-food 2 (P-F2), post-predator exclosure + food (P-PE+F), food addition A (+FA), and food addition B (+FB)

[†] not food supplemented in 1997

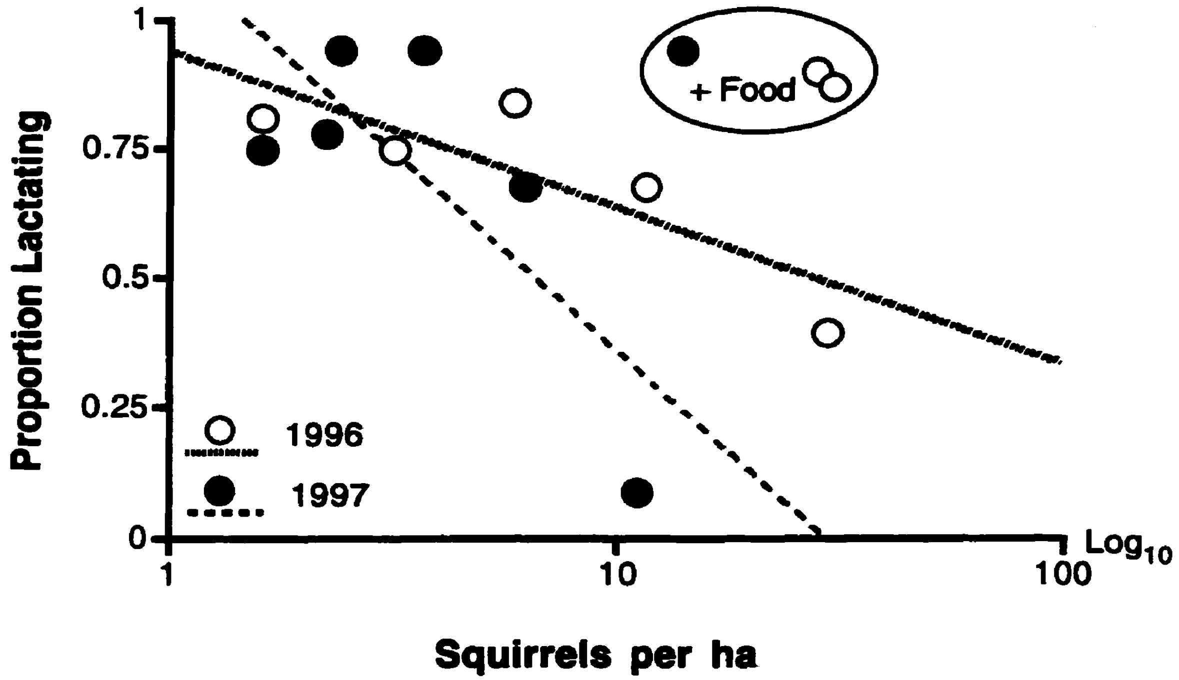


Figure 2.4 Proportion of adult female arctic ground squirrels with litters prior to weaning as indicated by signs of lactation. Lactation rate declines with density but remains ≥ 68% for all populations except the densest populations in both years. Food supplemented sites were not included in regression.

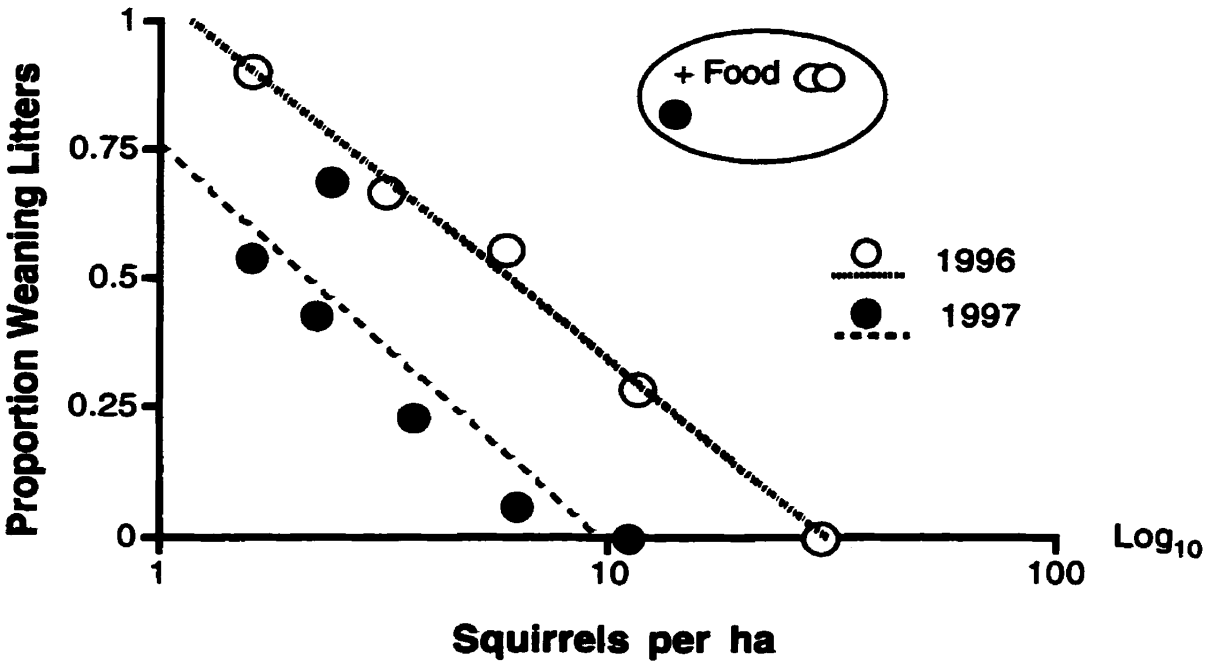


Figure 2.5 Proportion of adult female arctic ground squirrels weaning a litter plotted against spring population density for each site during 1996 and 1997. Proportion weaning litters maintains the same strength in density dependence in both years (i.e. similar slopes). However, weaning rate averaged 30% lower (i.e. different y-intercepts) in 1997 compared with 1996 when corrected for density. Food supplemented sites were not included in regression.

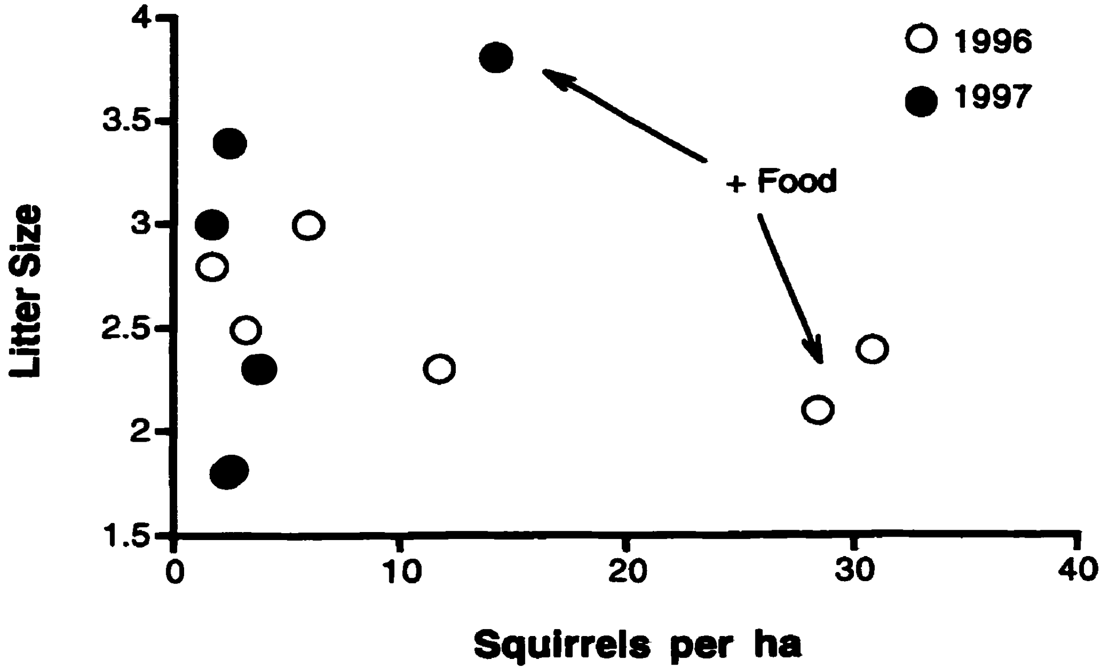


Figure 2.6 Estimates of average litter size at emergence for litter sizes ≥ 1. Sites where all litters failed are not included.

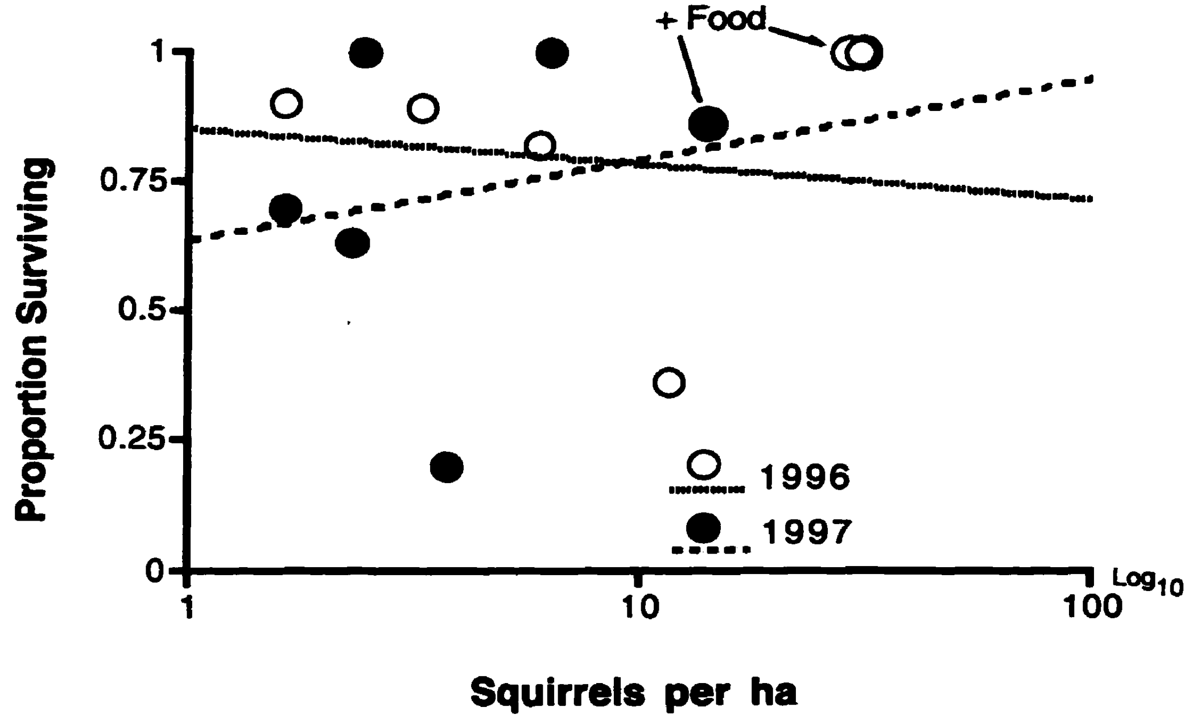


Figure 2.7 Mean proportion of adult female arctic ground squirrels surviving a 16-week period during the summer active season in relation to spring population density for that site during 1996 and 1997.

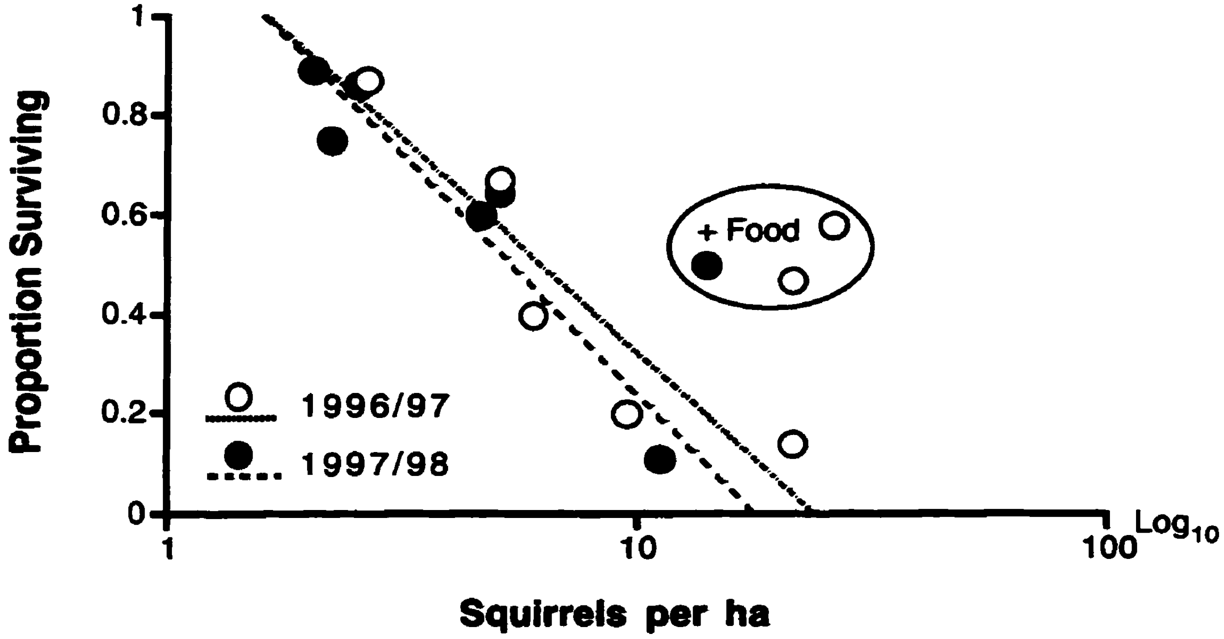


Figure 2.8 Proportion of adult female arctic ground squirrels surviving the winter hibernation periods (September – May) 1996 – 1997 and 1997 – 1998 plotted against late summer (late July – early August) population density. Proportion surviving hibernation has the same strongly density-dependent relationship in both winters and shows the same relationship in both winters. Food supplemented sites were not included in the regression.

because survival was greater in two lower density, non-fed populations in 1996 and five lower density, non-fed populations in 1997 (Figure 2.8).

Adult Dispersal

During 1996 and 1997, 79 and 51 adult female squirrels respectively, were radio-tracked among all sites for evidence of dispersal. Astonishingly, none of the 130 squirrels dispersed outside of the study sites despite severe competition for the limited resources owing to the high densities on some sites. This emphasizes the strong attachment of adult female ground squirrels to their burrow systems.

Contribution to rates of increase

Because weaning rate and overwinter survival showed strong density dependence, I entered both as independent variables into a multiple regression to determine their relative contribution to the annual rates of population increase. Annual rates of increase were significantly predicted by combined overwinter survival and weaning rate ($R^2 = 0.90$, n = 11, $P < 0.001$). However, weaning rate explained only 3% of the variability in annual rate of increase ($t = 1.55$, df = 10, $P = 0.16$) whereas overwinter survival explained 87% of the annual rate of increase ($t = 11.27$, df = 10, $P < 0.001$). Therefore, overwinter survival was the critical factor determining the rate of decline in the experimental populations as they converged towards control densities.

Changes in mass and body condition

Because the average mass of adult females emerging after hibernation varied interactively among sites and years (two-way ANOVA, year × site: $F_{10,666} = 5.369$, $P < 0.001$), I investigated each variable (year and site) separately to determine the source of the interaction. Differences among sites occurred in all three years (Table 2.2). During the first post-experimental year (1996), female squirrels on former food supplemented sites and on the continued food supplemented site had greater mass than those on control sites (Figure 2.9, Table 2.2) thus indicating a carry-over effect of the treatments from the previous year (Karels et al. 2000). However, by the spring of 1997, squirrels on all sites had similar mass (397-420 g), except for squirrels on the food supplemented site (Food addition A) which were 18 to 25% heavier. Average mass of squirrels in all sites were lighter in 1997 than in 1996 except for controls (Figure 2.9). Average mass remained similar among sites in the spring of 1998 and similar to that of spring 1997, with the exception of those on the food supplementation grid which were 25% lighter than they were in spring 1997. There was also a slight (14%) but non-significant increase in mass of squirrels on the post-food 2 (Figure 2.9).

The mass of adult female ground squirrels in the fall, just prior to hibernation, also varied among sites but interactively with years (two-way ANOVA, year × site: $F_{5,211} = 5.982$, $P < 0.001$). Despite the large degree of differences in population density (Figure 2.2) among the sites, fall body mass of squirrels was similar (Figure 2.9, Table 2.2), with the following exceptions. Squirrels on the post-food 1 site were significantly lighter than those on most sites and squirrels on the Food addition A site were significantly heavier than those on most sites (Table 2.2). Most remarkably, female squirrels on the post-predator exclosure + food site in the fall of 1996 had similar body mass (526 ± 12g) to those on controls (539 ± 14g) in spite of the 19-fold difference in population density during the spring. In the fall of 1997, body mass of female squirrels was similar on all sites with exception of squirrels on the post-food 2 site which were significantly heavier (21%) than those on the post-predator exclosure + food site.

Body condition of adult females was estimated from mass measured at parturition (late-May) (Dobson and Michener 1995). Since structural size (zygomatic arch breadth) varies among individuals among sites (two-way ANOVA: $F_{5,475} = 4.84$, $P < 0.001$) and between years (two-way ANOVA: $F_{5,475} = 4.93$, $P = 0.03$) and is a good predictor of body mass ($y = 28.1x - 546.3$, $r^2 = 0.29$, $n = 486$, $P < 0.001$), condition was estimated from the residuals of body mass regressed on structural size (zygomatic arch) (Dobson et al. 1999).

Body condition varied significantly among sites but there was significant reduction in body condition among all sites, with some sites declining more than the rest (post-predator exclosure + food, post-food 1, post-food 2) (Figure 2.910). This lead to a significant interaction between site and year (Table 2.3). During the first post-experimental year (1996), there were no significant differences in the condition of female squirrels between controls and any of the post-experimental sites (Table 2.3) despite a 2- to 19-fold difference in density. Only squirrels on the food addition sites were in significantly better condition than those on controls (Table 2.3), but supplemented food did not prevent the condition of females declining from 1996 to 1997 (Figure 2.10). Declines in condition were most pronounced (43-116g) in squirrels on the previously food supplemented sites, with smaller declines in squirrel condition on the predator exclosure (10g) and controls (6g). By spring of 1997, only squirrels on post-food 1 and

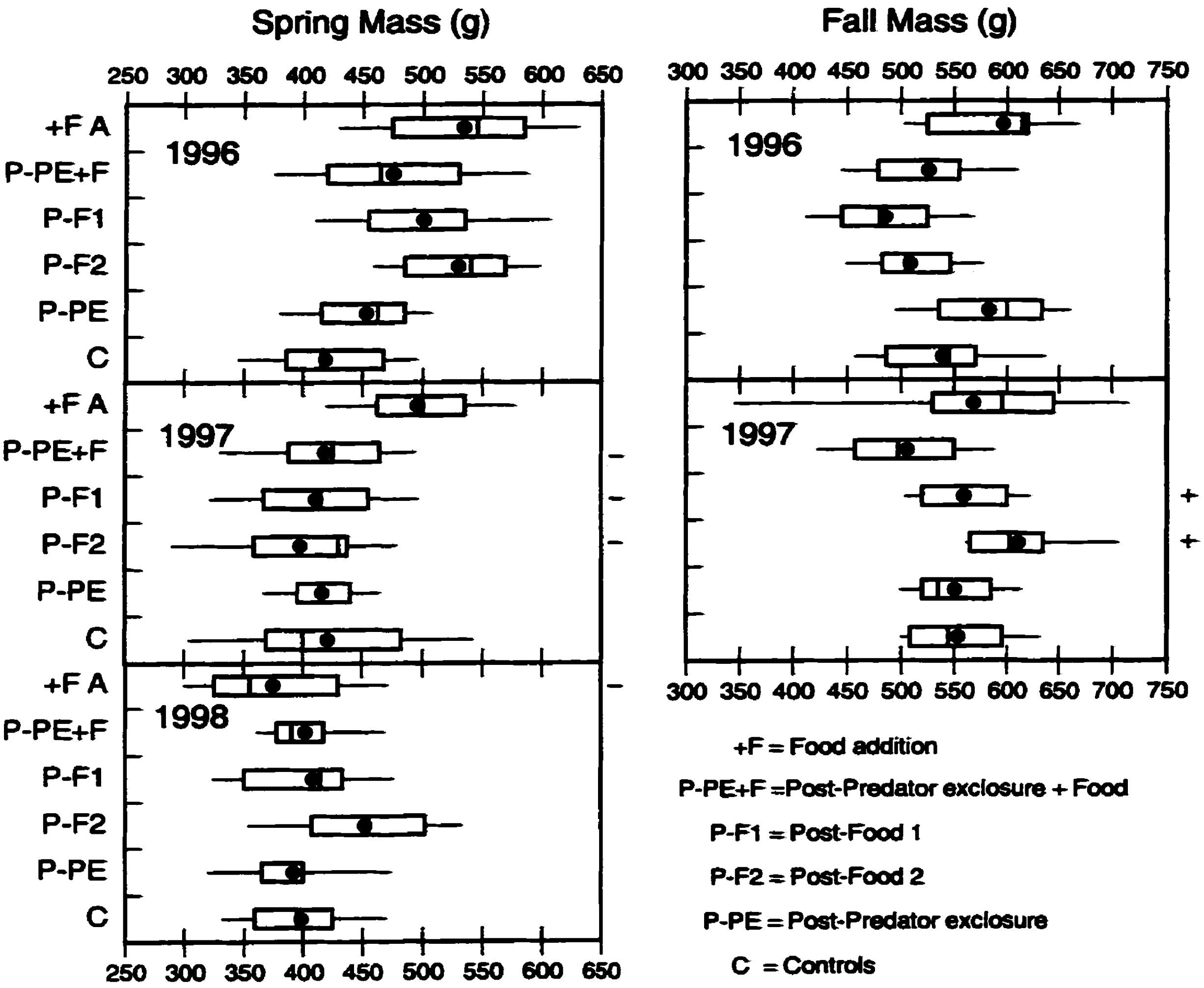


Figure 2.9 Early spring and fall mass (g) of adult female arctic ground squirrels on controls and experimental sites from 1996 to spring 1998. The left, right and line through middle of each box represent the 25th, 75th, and 50th percentiles. Whiskers from left to right represent the 10th and 90th percentiles. Mean mass is represented by (●). The symbols (+) and (-) on the right border of the graph, represent a significant increase or decrease (Tukey-Kramer post-hoc test) from previous year. Statistical comparisons among sites are given in Table 2.2

Table 2.2 ANOVA table of comparisons of mass of adult female arctic ground squirrels among six sites separated by year and season. Identical letters represent non-significant differences (Tukey-Kramer post-hoc test) in mass among sites for each year and season. Site names for abbreviation are given in Figure 2.9.

Site	1996			1997			1998		
Spring	**F**	**df**	**P**	**F**	**df**	**P**	**F**	**df**	**P**
	20.56	5	<0.001	6.77	5	<0.001	2.77	5	0.02
+ Food A		a			b			a	
P-PE+F		c			a			a b	
P-F1		a			a			a b	
P-F2		a c			a			b	
P-PE		b c			a			a b	
Control		b			a			a	
Fall	**F**	**df**	**P**	**F**	**df**	**P**			
	10.08	5	<0.001	3.67	5	0.005			
+ Food A		b			a b				
P-PE+F		a c			b				
P-F1		c d			a				
P-F2		d			a b				
P-PE		a b			a b				
Control		a b			a b				

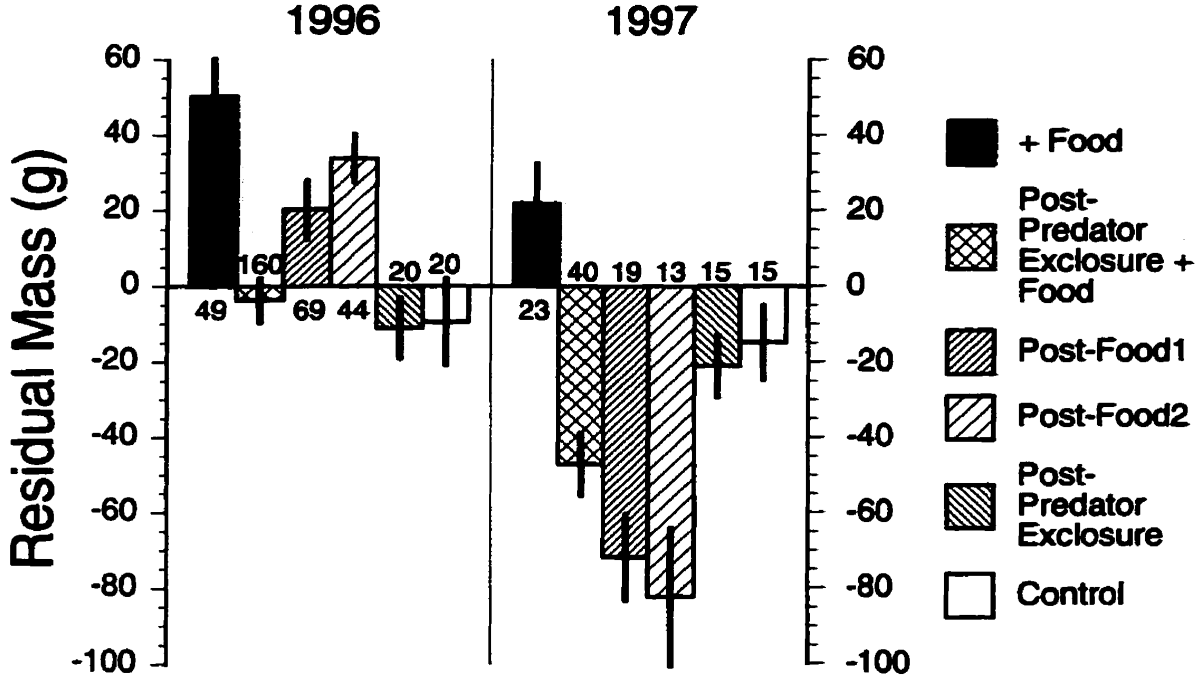


Figure 2.10 Comparison of condition as measured by residuals of mass (g) derived from linear regression ($y = 28.1x - 546.3$, $r^2 = 0.29$, $n = 486$, $P < 0.001$) of mass at parturition on zygomatic arch breadth of arctic ground squirrels among all post-experimental sites and controls from 1996 to 1997. Sample sizes are indicated at the base of column.

Table 2.3 ANOVA table of comparison of condition as measured by residuals of mass (g) of adult female arctic ground squirrels among post-experimental sites and controls from 1996 to 1997. Identical letters represent non-significant differences (Tukey-Kramer post-hoc test) in residual mass among sites separated by year.

Factor	***F***	**df**	***P***
Year	46.68	1	< 0.001
Site	10.26	5	< 0.001
Year × Site	6.05	5	< 0.001

Site	**1996**	**1997**
+ Food	c	b
Post-Predator Exclosure + Food	a	a,c
Post-Food 1	a,b,c	c
Post-Food 2	b,c	c
Post-Predator Exclosure	a,b	a,b
Control	a,b	a,b

post-food 2 sites were significantly different than controls, being an average of 56 g and 57 g lower in condition than those on controls, respectively (Figure 2.10).

Herbivore impacts on vegetation

The standing crop biomass of the ten plant species (*Achillea borealis, Antennaria* sp., *Epilobium angustifolium, Mertensia peniculata, Solidago* sp., *Festuca altacia, Astragalus*, sp, *Hedysarum* sp., *Lupinus arcticus*, and *Oxytropis* sp.) separated by sites, and herbivore treatment (open to herbivory or herbivores excluded) are shown in Figure 2.11. When open to herbivory, differences in plant abundance among the three plant groups varied separately by site and by year as indicated by the significant interactions (Table 2.4). However, when herbivores were excluded the interaction between plant group and year disappeared, indicating that herbivores were responsible for the variation in differences among plant groups over both years (Table 2.4). The significant interaction between site and year in the absence of herbivores (Table 2.4) indicated that there were differences in the biomass of vegetation among sites and years independent of herbivory caused by hares and squirrels.

The sources of the complex interactions among years, plant groups, and sites shown in Table 2.4 were revealed by comparing the number of plots that had less plant biomass than the paired plot where herbivores were excluded (Table 2.5). There was no loss of plant biomass owing to herbivory on control sites. On more densely populated sites, all three plant groups showed evidence of herbivory with the strength of herbivory generally increasing as ground squirrel population density increased. Intensity of herbivory among the plant groups was ranked as follows: legumes > forbs > grass.

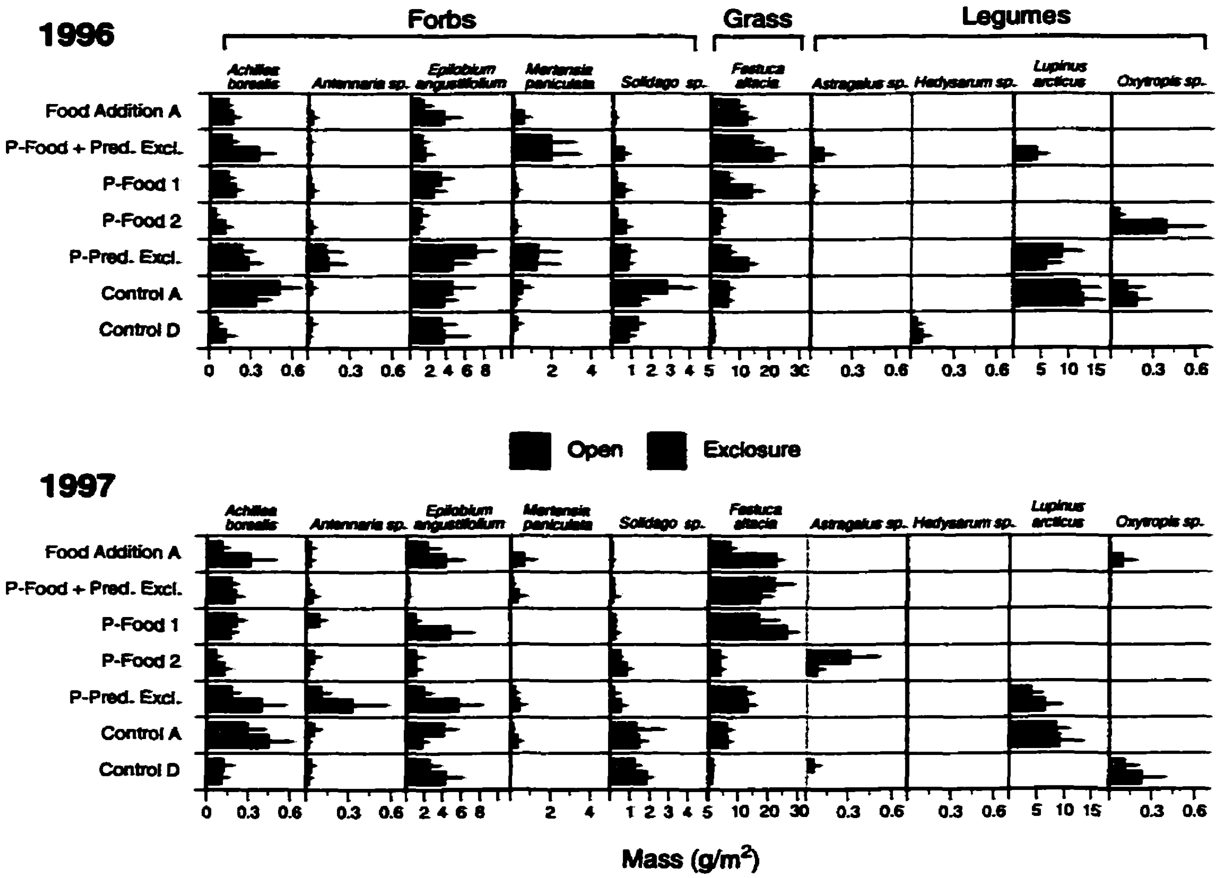


Figure 2.11 Standing crop dry-weight biomass (g/m^2) of ten plant species commonly found in the diet of arctic ground squirrels near Kluane, Yukon. Plants were clipped at ground level during late July from thirty paired 0.09 m^2 plots on each site. One plot from each pair was enclosed within a wire fence (2.54-cm mesh) to exclude herbivory from squirrels and hares.

Table 2.4 ANOVA table of comparison of standing crop dry-weight biomass among three plant groups (grass, forbs, and legumes), sites, and years (1996 and 1997) within paired 0.09-m^2 plots excluding and open to squirrel herbivory.

Factor	*F*	df	*P*
Exclosure			
Site	33.81	6	<0.001
Year	0.001	1	0.97
Plant Group	1009	2	<0.001
Site × Year	3.016	6	0.006
Site × Plant Group	18.29	12	<0.001
Year × Plant Group	1.044	2	0.35
Open			
Site	36.78	6	<0.001
Year	1.235	1	0.27
Plant Group	1113	2	<0.001
Site × Year	1.208	6	0.30
Site × Plant Group	20.42	12	<0.001
Year × Plant Group	4.075	2	0.017

Legume herbivory was extremely intense on sites with high squirrel density such that no legumes were found in any of the plots within the two highest-density non-supplemented sites (post-predator exclosure + food and post-food 1) by 1997. Although no legumes were observed on the Food Addition A site in either year, it is possible that legumes were entirely removed prior to 1996 in the same manner that they were removed from other sites.

The most abundant legumes were lupines (Figure 2.11). Though I did not collect biomass estimates prior to 1996, a pilot study conducted in 1995 contrasted lupine herbivory (as measured by counts of lupine petioles) on twelve 1-m^2 plots on one control (control A) with twelve 1-m^2 plots on the predator exclosure + food treatment. Each plot was paired with an adjacent and equivalent sized herbivore exclosure. Petiole counts from this pilot study were compared with petiole counts on the thirty 0.09-m^2 plots constructed in both 1996 and 1997 and indicated that herbivory of lupines on the predator exclosure + food intensified on this site after 1995 (Figure 2.12). Thus, there was a significant interaction between site and herbivory treatment (Table 2.6). On the control site, the number of lupine petioles per m^2 did not differ between plots open to herbivory and those from which herbivores were excluded or among years (Table 2.6).

Although petiole counts in 1995 did not reveal a significant difference between the herbivore exclosure and open plots on the predator exclosure + food site, signs of herbivory such as leaves nipped off or missing revealed that herbivory was still intense there. In 1995 on the predator exclosure + food, 89% (N = 888) of lupine petioles in areas open to herbivores showed signs of herbivory. In contrast, only 17% (N = 1238) of those lupine petioles on controls showed signs of herbivory. Signs of herbivory were not

Table 2.5 Comparison of the dry-weight biomass of three vegetation types within 0.09 m^2 plots open to herbivory with paired plots excluding vertebrate herbivores. Values below the symbols '–' and '+' are the number of plots in which plant biomass is less than or greater than biomass within the paired herbivore exclosure plot. All values below the = symbol are the number of plots in which the vegetation type was absent from both of the paired plots. The *P*-value denotes significance at the $\alpha = 0.003$ level calculated by one-tailed Wilcoxon's signed-ranks test for paired observations. Sites are sorted from greatest to least in density of ground squirrels. Site abbreviation descriptions are found in Table 2.1.

Site	**Forbs**				**Grass**				**Legumes**			
1996	**-**	**+**	**=**	***P***	**-**	**+**	**=**	***P***	**-**	**+**	**=**	***P***
+Food A	10	3	1	0.013	9	5	0	0.36	0	0	14	-
P-PE+F	19	9	2	0.086	22	8	0	0.002	15	2	13	<0.001
P-F1	17	10	3	0.50	20	10	0	0.032	5	0	25	0.042
P-F2	13	4	10	0.061	9	9	9	0.74	3	2	22	0.50
P-PE	9	19	3	0.12	18	10	2	0.034	5	7	17	0.39
Control A	10	17	3	0.27	14	13	2	0.96	12	6	10	0.42
Control D	11	17	2	0.12	12	12	6	0.61	3	1	26	0.27
1997	**-**	**+**	**=**	***P***	**-**	**+**	**=**	***P***	**-**	**+**	**=**	***P***
+Food A	11	4	0	0.13	12	3	0	0.009	0	0	15	-
P-PE+F	16	8	6	0.17	13	17	0	0.69	0	0	30	-
P-F1	15	13	2	0.46	19	10	1	0.017	0	0	30	-
P-PE	19	7	5	0.009	12	18	0	0.64	5	4	20	0.68
P-F2	11	4	15	0.19	9	12	9	0.88	2	2	26	0.47
Control A	12	15	3	0.44	11	17	1	0.37	6	8	14	0.60
Control D	14	12	4	0.40	11	16	3	0.61	2	2	26	0.72

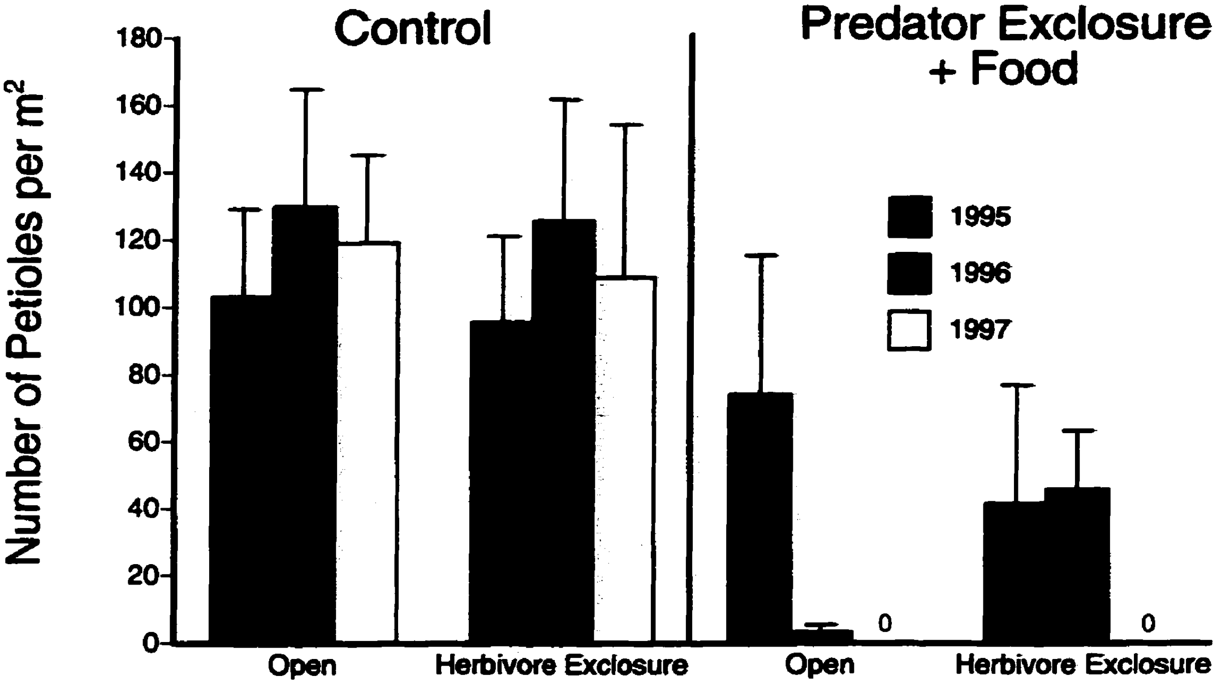


Figure 2.12 Lupine abundance (number of petioles per m^2 ± S.E.) within plots open to and excluded from herbivory on two sites (control and predator exclosure + food). Counts were conducted at twelve stations with paired 1-m^2 open and exclosure plots in 1995, before the predator exclosure + food treatment was dismantled, and in thirty stations with paired 0.09-m^2 open and exclosure plots in 1996 and 1997, after the predator exclosure + food treatment was dismantled. There were no lupines found on the post-predator exclosure + food site in 1997.

Table 2.6 ANOVA table of comparison of abundance of lupines between sites (control and predator exclosure + food), years (1995 and 1996), and presence of herbivory (present or absent). Because lupines were entirely absent from the predator exclosure + food in 1997, statistical analysis on lupine abundance was conducted only on the control site to determine if lupine abundance changed throughout a three year period (1995 - 1997).

Control and Predator Exclosure + Food (1995 and 1996)

Factor	*F*	df	*P*
Year	9.96	1	0.002
Site	9.36	1	0.003
Herbivory	1.78	1	0.18
Year × Site	0.37	1	0.54
Year × Herbivory	0.05	1	0.83
Site × Herbivory	4.03	1	0.047

Control (1995-1997)

Factor	*F*	df	*P*
Year	1.79	2	0.17
Herbivory	0.38	1	0.54
Year × Herbivory	0.09	2	0.92

entirely caused by animals squirrel-size or larger since there were still signs of herbivory within the herbivore exclosures perhaps caused by voles. However, there were two instances of a squirrel digging into the same herbivore exclosure on the predator exclosure + food site. Nevertheless, on the predator exclosure + food site, the frequency of herbivory within the herbivore exclosures was significantly lower (14%) than outside of the exclosure (N = 976; $G = 1138$, df = 1, $P < 0.001$). On the control, the frequency of herbivory within the herbivore exclosures was not significantly different (4%) from that outside of the exclosures (N = 1147; $G = 2.8$, df = 1, $P = 0.09$).

Environmental changes

In order to determine which environmental factors influenced reproduction in 1996 and 1997; I compared the previous winter's temperatures, previous winter's snow depths, spring to fall temperatures, and rainfall between years and with the 30-y long-term average. Spring temperatures during 1996 were similar to the 30-y long-term average. In 1997 spring and summer weather conditions appeared to be advanced by one month in comparison with normal conditions (Figure 2.13). Temperatures were 8°C and 7°C higher than normal for April and May, respectively and June rainfall was twice that of normal and seven times that of 1996. During winter, only January temperatures departed greatly from normal. In 1996, January temperatures were approximately 10°C lower than normal whereas in 1997, January temperatures were approximately 13°C above normal. Snowfall arrived early in 1995 such that by November there was 36% more accumulated snow than normal. Thereafter snow depth remained similar to that of

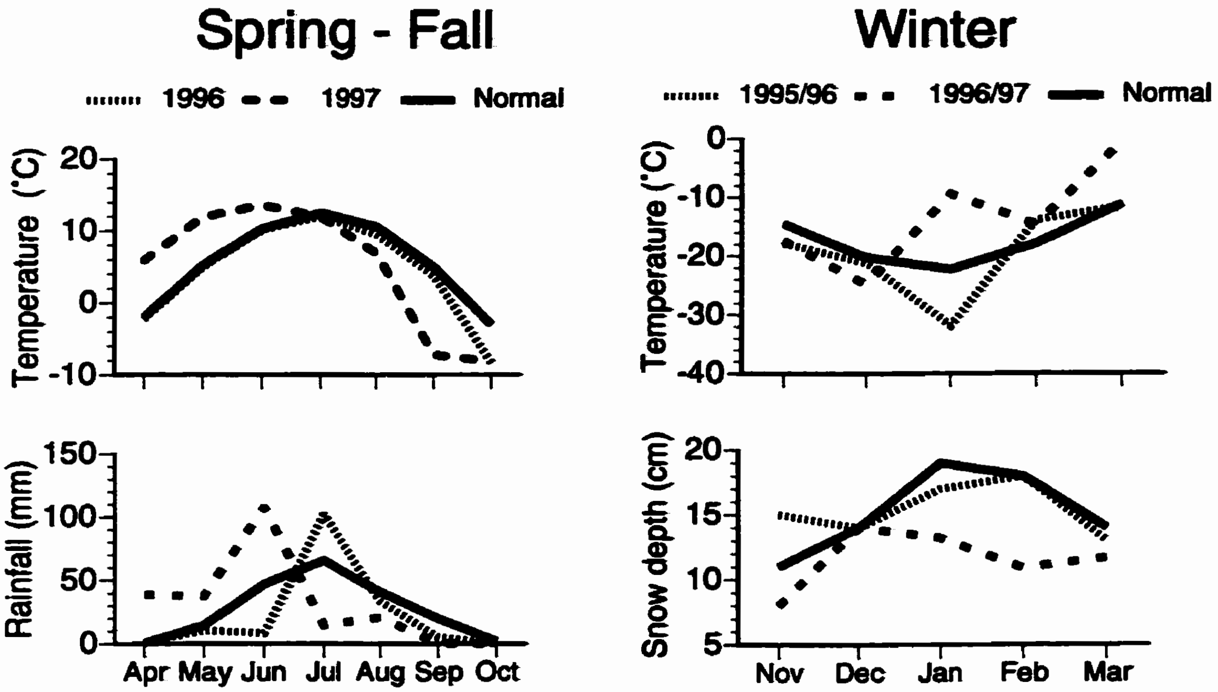


Figure 2.13 Plots of monthly means and 30-year averages of temperature, rainfall, and snow depth from data collected from Burwash Climatological Weather Station, Burwash Yukon.

the long-term average. Snow depth during the winter of 1996/97 was unusually low. Total snow depth was 27%, 31%, and 29% less than normal for the months of November, January, February, respectively. December snowpack was similar to the normal.

Although spring conditions during 1997 was warmer and wetter, the initiation of the growing season as determined from aspen leaf appearance (May 25), did not differ markedly from that of 1996 (May 27).

Discussion

The convergence of experimental arctic ground squirrel densities to those on controls within two years after removal of predator exclosures and food supplementation (Figure 2.2) is the strongest form of evidence that their population densities are regulated (Murdoch 1970; Sinclair 1989; Caughley and Sinclair 1994; Harrison and Cappuccino 1995; Cappuccino and Harrison 1996). In order for populations to be regulated, the rate of change in numbers must be density dependent (Sinclair and Pech 1996). In my study, the rates of population change within the experimental sites (post-treatment) and controls were strongly density dependent (Figure 2.3). However, the density dependence paradigm is often criticized because it fails to recognize the mechanisms or relevant variables that cause regulation since density itself is not a mechanism (Krebs 1995). During my study, the mechanisms of regulation were intraspecific competition for food in the late stages of reproduction that influence the proportion of females weaning litters (Figure 2.5) followed by intraspecific competition for food resources that influence overwinter survival (Figure 2.8). Intraspecific competition for food was the underlying factor determining density dependence for two reasons. First, natural food sources declined with increasing squirrel density (Figure 2.1, Table 2.5, Figure 2.12). Second, supplemental food reduced the rate of decline (Figure 2.2, Figure 2.3) by improving weaning rate and overwinter survival relative to population density (Figure 2.5, Figure 2.8). The strength of density dependence in weaning rate remained similar from 1996 to 1997. However, decreased snow depth during the winter of 1996/97 relative to 1995/1996 (Figure 2.13) was associated with a decline of 30% in weaning rate regardless of population density (Figure 2.5). Therefore, changes in ground squirrels reproduction are clearly driven by simultaneous density-dependent and density-independent processes.

Predators produced density-independent variation in survival among sites but that variation was not important during this study because overwinter survival and reproduction explained (90%) of the yearly change in population densities. This is not to claim that predators were unimportant, as predators have been clearly shown to interact with food in limiting arctic ground squirrel populations (Karels et al. 2000). However, limiting factors are not necessarily regulating (Sinclair 1989) and the most likely scenario is that predators act as a density-independent variable influencing reproduction which is also strongly influenced by intraspecific competition. However, the sublethal effects of predators on reproduction are difficult to detect when reproduction is also dependent on food abundance and population density. Testing this hypothesis would require combining squirrel density manipulation and predator manipulation.

Reproduction

In mammals, the cost of gestation is exceeded by the cost of lactation and this increases towards weaning (Millar 1977) such that mass loss of the mother is evident during the late stages of lactation (Kiell and Millar 1980; Clutton-Brock et al. 1989;

Humphries and Boutin 1996; Millesi et al. 1999). Fluctuating environmental conditions that might reduce resource availability will have the greatest negative impact on female reproduction during the energetically exhausting lactation period rather than during the gestational period. My earliest evidence that females had been pregnant was derived from signs of lactation because I was not able to determine if litters were lost *in utero*. Nevertheless, the proportion of females showing evidence of lactating was consistently high (> 75%) across a wide range of population densities except in populations with densities exceeding 10 squirrels per ha without supplemental food (Figure 2.4). Thus, most of the differences among the sites in the proportion of females weaning their litters resulted from losses of entire litters during lactation, thereby producing a strong relationship between weaning rate and population density driven by competition for food resources (Figure 2.5). When I continued to supplement populations with food, weaning rates showed no evidence of being influenced by population density (Figure 2.5) and remained high (> 82%) and similar to weaning rates on the same site (predator exclosure + food) prior to 1996 when the food addition was still in progress (Karels et al. 2000). In a similar study on Columbian ground squirrels, Dobson and Kjelgaard (1985b) supplemented food to a high and a low elevation population for 3 years producing a 4.9 and 5.5-fold increase in population density. Dobson (1995) continued to monitor these populations after food addition was ceased and found that in the first year, weaning rate dropped 33% and 52% within the high and the low elevtion populations, respectively. Thus, intraspecific competition for food resources influencing weaning rate applies to Columbian ground squirrels as well as to arctic ground squirrels.

Food addition increased the mass of females on all food-supplemented sites relative to control sites during 1995 (Karels et al. 2000) and this effect carried over into the first post-experimental year (1996) with squirrels emerging from hibernation with greater mass (Figure 2.9). But this effect did not follow through to parturition, as female squirrel condition at parturition was similar among post-experimental sites and controls (Figure 2.10, Table 2.3) despite 2- to 19-fold differences in population density. Hence weaning success among the sites was not dependent on condition at parturition but rather on density-dependent effects (competition for food resources) occurring during the late lactational period.

On all sites from 1996 to 1997, there were declines in the average squirrel spring mass (Figure 2.9), condition at parturition (Figure 2.10), and weaning rate independent of density (Figure 2.5). Remaining fat stores after hibernation are used to supply energy for reproduction (Thompson et al. 1993). However, Kiell and Millar (1980) showed that for female arctic ground squirrels, stored fat resources contribute only about 31% of the energy demand of a litter with the balance having to be obtained from over-wintered forage and emerging fresh vegetation. Variation in food resources between years did not explain the decline in weaning rate for the following reasons: initiation of the growing season did not differ greatly between years (1996 = May 25, 1997 = May 27); abundance of natural forage did not differ between years (Figure 2.11, Table 2.3); there was no detectable changes in herbivory on controls and the post-predator exclosure (Table 2.4); and weaning rate declined (7%) in the presence of supplemented food despite much lower densities in 1997 (55% lower than in 1996). Alternatively, fat stores retained from the previous fall may have contributed to the greater reproductive success of females in

1996 relative to 1997. In arctic ground squirrels, mass loss over winter is dependent on ambient temperature of the hibernaculum (Anufriev and Akhremenko 1990). Though January's mean monthly temperature was colder during 1995/96 (Figure 2.13) than during 1996/97, snow depth was 25-40% greater during 3 months in 1995/96 than in 1996/97. Accumulated snow provides an insulative layer between the ground and fluctuating ambient temperatures (Marchand 1991; Buck and Barnes 1999b). Hibernating squirrels during the winter of 1995/1996 should have been better shielded from the ambient above ground air temperatures than those hibernating in 1996/97 thus the former should have expended less energy overwinter. Retained fat reserves from over the winter would be advantageous for reproduction in the following season.

Overwinter survival

Overwinter survival acted in a strong and constant density-dependent manner over both winters (Figure 2.8) and explained 87% of the rate of population change converging densities on experimental treatments with those on control sites. Thus, overwinter survival was the most critical factor regulating arctic ground squirrel populations.

Competition for food resources is the only plausible explanation for negative relationship between overwinter survival and population density for four reasons. Hibernacula sites were not limiting since population densities on the predator exclosure + food site during the fall of 1995 were 16-fold that of controls and the over winter survival rate was not less than that of controls (67% vs. 52% respectively) (Karels et al. 2000). Second, there was competition for available forage since herbivory intensified with increasing ground squirrel density (Table 2.5). Third, prior to 1996, when treatments were still operative, overwinter survival on food supplemented sites was comparable to controls (≈ 63%) (Karels et al. 2000) and declined only after food was removed. Fourth, continued supplementing of rabbit chow maintained higher overwinter survival on high-density populations (food addition A and B) than on non-fed high-density sites (post-predator exclosure + food) (Figure 2.8). However, supplemented food resources (in the form of rabbit chow) seemed to play only a partial role in overwinter survival, at least at high densities. Continued food supplementation on segments of the post-predator exclosure + food site (food addition A and B) was not sufficient to prevent these fed populations from rapidly declining in numbers (51% food addition A and 64% food addition B from 1996 to 1997 and 60% food addition A from 1997 to 1998) (Figure 2.2) owing to low overwinter survival (Figure 2.8). Therefore some other resource must have been limiting.

Successful hibernation in ground squirrels is dependent on the quantity of accumulated fat reserves (Murie and Boag 1984) obtained by intense foraging during the brief period after reproduction and before hibernation (Armitage et al. 1976; Kenagy 1987). However, fat quantity alone is not sufficient for successful hibernation. Before entering hibernation, squirrels on previously food supplemented sites were similar in mass to those squirrels on non-supplemented sites (Figure 2.9, Table 2.2) yet they suffered higher overwinter mortality than their non-supplemented counterparts. The most extreme example from my study occurred on the post-predator exclosure + food site during the fall of 1996. Adult female squirrels on that site had similar pre-hibernation body mass to controls (526 ± 12g vs. 539 ± 14 g respectively) but had extremely poor over winter survival relative to females on controls (0.14 vs. 0.88 proportion surviving, respectively).

The composition of fatty acids within white adipose tissue is critical in regulating metabolic and thermoregulatory processes during hibernation (Thorp et al. 1994; Florant 1998). Polyunsaturated fatty acids (i.e. linoleic and α-linolenic fatty acids) lower the melting point of depot fats (Mead et al. 1986; Pond 1998) such that when supplemented to sciurid hibernators they maintain lower minimum body temperatures, lower metabolic rates, and longer bouts of torpor (Geiser and Kenagy 1987; Frank 1992; Geiser and Kenagy 1993), resulting in reduced energy expenditure and promoting increased over winter survival. Animals can not synthesize these polyunsaturated fats (Lehninger 1982; Pond 1998) so any in their depot fat composition are derived from their diet (Geiser 1990). For ground squirrels, this means their required supply of polyunsaturated fatty acids is obtained from their food plants in which fatty acid concentration varies among species, parts of the plant, and seasonally (Harwood and Geyer 1964; Florant et al. 1990; Hill and Florant 1999). Frank (1994) showed that golden mantled ground squirrels (*S. lateralis*) select diets based on their linoleic acid content to maintain a concentration of 23-25 mg of linoleic acid per gram of diet, therefore demonstrating that fatty acid content in plants is a factor determining food preferences in ground squirrels.

Legumes (primarily lupines since other types were relatively rare) were so heavily grazed that they were extirpated from sites with high ground squirrel densities (Figure 2.12, Table 2.5). My measurements of herbivory do not differentiate among the impacts of the different herbivores in the study area (i.e. ground squirrels, hares and voles). However differences in ground squirrel density are the only explanation for the differences in herbivory among the sites since hares, close to their maximum cyclic density, were abundant everywhere (C. J. Krebs pers. comm.), and voles were scarce (R.

Boonstra pers. comm.). Legumes are a major component of ground-dwelling sciurid diets (Hansen and Ueckert 1970; Hansen 1975; Blumstein and Foggin 1997), and in particular, lupines are highly preferred by arctic ground squirrels (Lincoln 1972; McLean 1985). When compared with other plants in the Kluane area, lupines have similar water and protein content, and higher fiber content (Hodges 1998; D. Hik in prep.). They also have higher concentrations of toxic alkaloids (Hansen and Johnson 1976; Majak et al. 1994; Panter et al. 1994). However, legumes are also known to contain high concentrations of polyunsaturated fats (Harwood and Geyer 1964), and for some species of lupines, high concentrations of polyunsaturated fatty acids are contained within flowers (*L. pribundus*) (Florant et al. 1990) and seeds (*L. albus, L. angustifolius* and *L. luteus*) (Yanez et al. 1983).

In summary, herbivory on legumes increased at the same time as overwinter mortality increased in a density-dependent manner. There was intense herbivory on legumes even when high protein rabbit chow was supplemented. Overwinter survival declined in the presence of supplemented chow. Legumes were the only group of plants extirpated from sites with high densities of ground squirrels. This evidence supports the hypothesis that the rate of overwinter survival is determined by the intensity of competition for plants with the limited essential fatty acids such that it is a mechanism by which arctic ground squirrel populations are regulated.

Density-dependent vs. density-independent factors

The hallmark of the density manipulation experiment is its ability to detect regulating factors while controlling for factors that vary temporally and independently of population density (i.e. density-independent effects). In my experiment, density-dependent reproduction (measured by the percentage weaning litters) (Figure 2.5) operated at the same strength over two years following the removal of the treatments. However, from 1996 to 1997 this relationship was shifted to the left (Figure 2.5) while maintaining the same strength in density dependence, such that for the same density of ground squirrels, reproduction was 30% lower in 1997 than it was in 1996 for the post-experimental sites and 7% lower for the food supplemented population. I attributed this difference to changes in overwinter environmental conditions (i.e. low snowpack in the winter of 1996/97) which negatively influenced ground squirrel reproduction through use of fat reserves independently of density and food resources. Had I been investigating density dependence without the use of the density manipulation experiment it is likely that I would have concluded that reproduction is governed by density independence or at best by density vagueness (Strong 1984) with little strength to discriminate between the two.

Density dependence is a necessary, but not a sufficient condition for population regulation (Turchin 1999). Populations rarely, if ever, maintain or achieve equilibrium (Sinclair 1996; Sinclair and Pech 1996). Stochastic events can induce fluctuations in populations that are independent of density leaving density-dependent factors to return populations back to their limit. Environmental fluctuations will have the same effect on rates of increase regardless of the size of the population. Environmental stochasticity may affect rates of population growth through changes in food resources or operate more directly on mortality. However, as Caughley (1994) stated, environmental variation simply adds to the background variation in rates of increase in natural populations over long time scales. Variation in snowpack acted as a stochastic event in my study. Without affecting overwinter survival, the reduction of snowpack in one year compromised reproduction at the onset of the reproductive period by reducing the base-line resource level in the form of fat reserves. Thereafter, the ability to attain the resource level necessary to bring a litter to weaning was determined by density-dependent food limitation. However, regardless of the density-dependent and -independent effects on reproduction, the primary force regulating these populations back to control densities was overwinter survival. Density-dependent weaning was a minor factor influencing the rate of change in ground squirrel populations as they returned to control densities. However, density-dependent weaning may become more important when populations are below equilibrium densities such as when predators reduce ground squirrel populations during the snowshoe hare decline.

Population dynamics of arctic ground squirrels in the boreal forest

It appears that arctic ground squirrel numbers are driven by a combination of fluctuating density-independent factors coupled with constant density-dependent factors that together produced the synchrony that was observed between ground squirrel and hare populations during one hare cycle (Boutin et al. 1995; Hubbs and Boonstra 1997). The decline in squirrel numbers occurred when predators were numerous (1991-1993) (Hubbs and Boonstra 1997; Byrom et al. 2000). During this period, predators acted directly through predation, but also indirectly by interacting with available food to reduce rates of reproduction (Hubbs and Boonstra 1997; Karels et al. 2000). When predators became scarce, ground squirrel numbers increased (Byrom et al. 2000; Karels et al. 2000) towards the new limits set by the conditions of the experimental treatments and the environmental conditions on controls. Food was determined to be the dominant factor limiting populations but the interaction between food and predators in affecting weaning rates (Karels et al. 2000) ultimately resulted in the marked differences in population densities among the experimental treatments and controls (Hubbs and Boonstra 1997; Karels et al. 2000).

The experimental manipulations of the Kluane Boreal Forest Ecosystem Project acted as a long-term perturbation that temporarily raised the equilibrium towards which arctic ground squirrel densities were attracted. The experimental populations reach their maximum densities after 10 years of manipulation (Hubbs and Boonstra 1997; Karels et al. 2000) but we could only identify factors as limiting and not regulatory. The intensive studies on ground squirrels did not start until several years after the manipulations began when the effects were already present (Hubbs and Boonstra 1997), thus we could not observe regulation directly. However, even if populations were studied at the initiation of the manipulations it is not obvious that density dependence would have been detected. Because of the different manipulations, each experimental site had a different equilibrium density, and thus regulation may have been difficult to observe in the presence of fluctuations in mortality from predation and from spring weather conditions. However, once manipulations ceased, strong regulation of numbers by overwinter survival was easily demonstrated because all sites then had a similar equilibrium density towards which the populations were drawn.

I assumed that the equilibrium ground squirrel density at Kluane was similar to that of the control populations because these fluctuated only slightly from 1996 to 1998 (1.6 ± 0.2 per ha to 2.0 ± 0.4 per ha) and these were at their highest densities since 1991 (1.8 ± 0.3 per ha) after the extreme lows in 1993 (0.7 ± 0.3 per ha) and 1994 (0.7 ± 0.4

per ha). Thus, I was unable to test how density dependent mechanisms operate at lower densities. However, once predators were few (1993), control populations showed density-dependent rates of increase over the next five years similar to the density-dependent relationship of the post-experimental treatments, but with greater variation (Figure 2.3). Therefore it appears that similar processes operated at lower densities. That is, overwinter survival working in concert with weaning rate through density-dependent food limitation determined the rate at which populations increased. However, as a consequence of the snowshoe hare cyclic decline, predators exert a periodic density-independent influence on mortality and reproduction that synchronize arctic ground squirrel populations with those of hares in the boreal forest.

Chapter 3

REPRODUCTIVE SUCCESS AND SURVIVAL OF FEMALE ARCTIC GROUND SQUIRRELS

Introduction

Negative effects of increasing population density on reproduction have been clearly demonstrated for many species of birds (Newton 1998) and mammals (Skogland 1983; Wauters and Lens 1995; Festa-Bianchet et al. 1998; Koskela et al. 1999). However, studies describing the mechanisms by which density dependence operates to influence reproduction in mammals are rare. There are a variety of density-dependent mechanisms that may reduce reproductive output of individuals. For example, increased population density may increase intraspecific competition for food resources (Skogland 1983; Arcese and Smith 1988; Festa-Bianchet et al. 1998; Koskela et al. 1999), force individuals into suboptimal habitat with lower resources or higher predation risk (Rodenhouse et al. 1997), increase the risk of infanticide (Agrell et al. 1998), or increase social stress (Christian and Davis 1964). Although reduction in reproductive output of a female may be caused by a physiological response to lack of nutrition or direct loss of young by infanticide or predation, reduction in reproductive effort may be an attempt by a female to increase her lifetime reproductive success (Williams 1966a,b).

Traditional life history theories assume that costs and benefits of reproduction vary only with age (Roff 1992; Stearns 1992). McNamara and Houston (1996) considered this approach limited and stressed that how an individual maximizes its lifetime reproductive fitness depends on its current physiological and environmental state. Individuals differing in mass or fat reserves (King et al. 1991; Doughty and Shine 1998; Festa-Bianchet et al. 1998), social status (Lundy et al. 1998), or parasite load (Newton 1998; Saino et al. 1999) may differ in reproductive ability. Likewise, temporal or spatial variation in the environment, such as predator abundance (Feltmate and Williams 1991; Oksanen and Lundberg 1995; Boonstra et al. 1998; Karels et al. 2000), habitat quality (Mallory et al. 1994; Riddington and Gosler 1995), or weather (Morton and Sherman 1978; Crête and Courtois 1997; Neuhaus et al. 1999) can also influence reproductive ability. The possibility that complex interactions among variables determine reproductive success or cause individuals to modify their reproductive effort presents a problem in state-dependent theory (Morris 1998).

Complexity among interacting state-variables can be overwhelming and difficult to tease apart; manipulating a variable may identify its contribution among the various state-variables possibly influencing the reproductive success of an organism. This is particularly important for studies in population ecology where the lack of manipulative studies has generated a call for more experimental studies (Harrison and Cappuccino 1995; Krebs 1995; Cappuccino and Harrison 1996; Murdoch and Nisbet 1996). In this study I manipulated population density to (1) determine how population density interacts with mass and age to influence reproductive success in female arctic ground squirrels (*Spermophilus parryii plesius*), and (2) determine how conditions of mass, age, reproductive expenditure, and population density influence squirrel survival. The density-manipulation approach (Harrison and Cappuccino 1995; Cappuccino and Harrison 1996) I used in this study created a series of increasingly poor environments.

This approach had two main advantages over traditional phenotypic correlation studies. First, because all measurements are made simultaneously in populations with different densities, each individual is used only once thereby preventing pseudo-replication (Hurlbert 1984). Second, density-dependent effects are not confounded by temporal changes in environment since all sites are within a small geographic area and thus should have similar weather patterns.

Arctic ground squirrels are the largest and most northern living ground squirrel in North America (Banfield 1974). They hibernate for 8-9 months each year (Hock 1960) emerging in early April to early May often from under snow cover and prior to the appearance of spring vegetation. Emergence dates are similar among arctic ground squirrels and the more temperate-dwelling species such as *S. columbianus, S. saturatus*, and *S. lateralis,* but environmental conditions are comparatively more severe for arctic ground squirrels (Buck and Barnes 1999a). Females are sexually receptive once per year for a 24 h period 3-4 days after emerging from hibernation (Lacey et al. 1997) but breeding can extend into early May owing to the variation in emergence dates (Lacey 1991). Despite the absence of fresh vegetation during the mating period, a high proportion of females attempt reproduction. Lacey (1997) found that 78% of females showed signs of having bred following oestrus. In my study area, an average of 81% of females on unmanipulated sites give birth as shown by signs of lactation (Karels et al. 2000).

The mass of adult female arctic ground squirrels is lowest at emergence from hibernation and increases gradually through the reproductive period until lactation (Buck and Barnes 1999a). After 25 days of gestation, young are born in an underground chamber during mid- to late May, but do not appear above ground for another 27 days when weaning occurs (Mayer and Roche 1954; Lacey et al. 1997). The energetic costs to the mother increase to a maximum during the later stages of lactation just before weaning (Millar 1977; Michener 1989). During this most energetically demanding period, female mammals generally allocate more energy to offspring than to their own maintenance, and therefore lose mass (Clutton-Brock et al. 1989; Humphries and Boutin 1996; Millesi et al. 1999). Once the young are weaned, a female arctic ground squirrel will accumulate mass rapidly in preparation for overwinter hibernation (late July to early August—McLean and Towns 1981; Buck and Barnes 1999a). As a result, adult female peak mass occurs one month prior to that of adult males in spite of the energetic demands of lactation on females (Buck and Barnes 1999a).

Environmental conditions such as drought, extensive rain, or extended winter are important factors in the reproductive success in ground squirrels and marmots (Morton and Sherman 1978; Phillips 1984; Smith and Johnson 1985; Van Horne et al. 1997; Schwartz et al. 1998; Neuhaus et al. 1999). In an earlier study in my study area, Hubbs and Boonstra (1997) found only 53.3% of female arctic ground squirrels gave birth following a spring of late heavy snow and delayed snowmelt compared with a 7-year average birth rate of 73.4 ± 4.3% (calculated from Hubbs and Boonstra 1997, Karels et al. 2000, this study). But it was unknown whether females in Hubbs and Boonstra's (1997) study failed to breed or whether they lost litters *in utero*. Neuhaus et al. (1999) studied reproduction of Columbian ground squirrels during dry, wet, and snowy spring conditions in southern Alberta in three consecutive years and found a 3, 29, and 66% loss of litters, respectively, during gestation showing that resorption or abortion of litters does occur when conditions are harsh. They also documented a further 15, 37, and 16% loss of litters, respectively in those same years, during lactation. Although survival of females decreased with increasingly bad weather, they did not compare survival of females that reproduced with those that did not. Therefore, there was no direct evidence that there was a survival cost of reproduction in their study. However, their study does show that ground squirrels commit themselves to reproducing early in the breeding season and then reduce that effort later possibly in response to environmental conditions.

If environmental conditions are poor (e.g. low food per capita or weather conditions that reduce foraging) and there is a phenotypic cost to reproduction, a female that reproduces may compromise her own survival. Reproduction may reduce body condition such that she must increase her foraging rate thus exposing herself to predators. Alternatively, if food is limited and reproduction has resulted in reduced body condition, a female may be unable to compensate for low fat reserves by intensive foraging prior to hibernation and thus has a higher risk of dying over winter. Furthermore, young produced in a poor environment may have a higher risk of mortality. If litter reduction is an adaptive strategy, then as population density increases (food per capita decreases), a female should reduce litter size accordingly, thereby increasing her probability of surviving to another reproductive season. Therefore, when food is limiting, females who do not reproduce should have a greater probability of survival than females that do reproduce.

If there are no phenotypic costs during any stage in reproduction under poor environmental conditions, then litter reduction may occur in proportion to the mother's nutrition. Thus, the variation in spring condition among females may show positive associations in fitness traits such as reproductive success being positively associated with survival. This phenomenon has been referred to by Dobson et al. (1999) as 'increasing returns'. In Columbian ground squirrels, Dobson et al. (1999) found that females with greater spring body mass gained more mass during reproduction and produced larger litters, and larger litters were associated with higher juvenile survival. They did not measure adult survival directly, but greater mass in Columbian ground squirrels has been shown to be associated with greater overwinter survival (Murie and Boag 1984). If arctic ground squirrels show 'increasing returns', then spring condition of adult females should be positively associated with the ability to wean young and survival such that reproductive females should have a greater probability of survival than do non-reproductive females with access to similar quantities of resources.

Study Site and Methods

Study area

My study was located along the Alaska Highway within the Shakwak Trench east of Kluane Lake in the southwestern Yukon Territory, Canada (61°N, 138°W). There are four major vegetation types in this valley: white spruce forests (*Picea glauca*) cover 50% of the area and have an understory of willow (*Salix* spp.) and birch (*Betula glandulosa*); shrub meadows of willow and birch cover 33%; and grass meadows cover 7% (Boutin et al. 1995); and trembling aspen (*Populus tremuloides*) stands (10%) are distributed among the other vegetation types (C. J. Krebs pers. comm.).

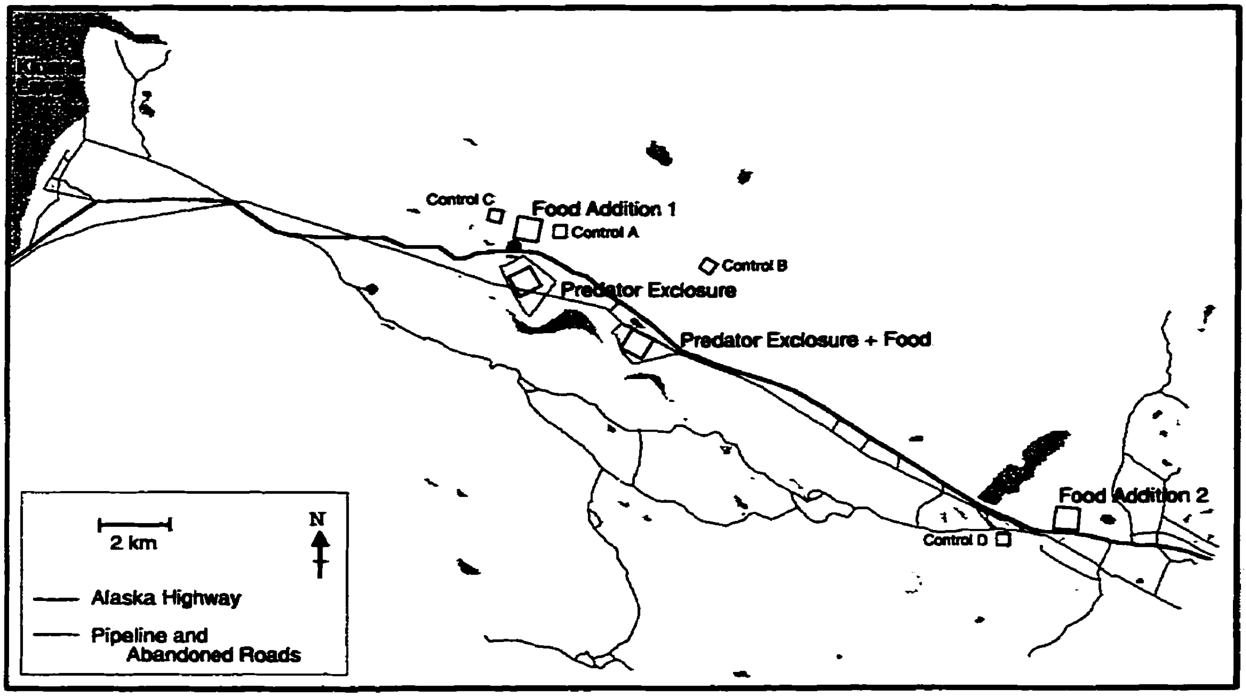


Figure 3.1 Location of experimental sites and controls of the Kluane Boreal Forest Ecosystem Project along the Alaska Highway in the south-west Yukon Territory, Canada. Experimental manipulations were terminated spring 1996.

The Kluane Lake area experiences a mean annual temperature of -3.9 ± 0.2 °C and receives an average of 284 ± 10 mm total annual precipitation (data from Burwash Landing Climatological Station 1967-1995). The climate is classified as cold continental and snow cover exists from October to early May (Boutin et al. 1995).

Experimental Design

I live-trapped ground squirrels on eight 8-10 ha areas. Four of these sites were unmanipulated controls (labeled Controls A-D, mean density = 1.6 ± 0.15 squirrels per ha) and the other four areas were previously manipulated as part of the Kluane Boreal Forest Ecosystem Project from 1987 to spring of 1996 (Krebs et al. 1995) (Figure 3.1). Details of these sites are listed in Chapter 2. Table 3.1 lists the spring population densities of arctic ground squirrels on each area when the experimental manipulations ceased in spring 1996. The differences in densities among these sites were created by the experimental manipulations of food and predators. When the treatments were removed, I examined the reproductive and survival responses of female arctic ground squirrels when the major factor that remained and differed among the sites was population density.

Population monitoring

In all years, I live trapped ground squirrels starting in late April to early May and ending in late August to monitor population density, survival, and reproductive status. Squirrels were captured using Tomahawk live traps (14 × 14 × 40 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with peanut butter. Traps were placed at

Table 3.1 Final spring population densities of arctic ground squirrels on experimental manipulations of the Kluane Boreal Forest Ecosystem Project completed in spring 1996. Experimental sites are described in Chapter 2.

Treatment	**Squirrels per ha**
Predator Exclosure	3.3
Food 1	5.9
Food 2	11.6
Predator Exclosure + Food	30.1

burrow sites to increase recaptures of individuals. Two or three traps were placed at burrow systems that had ≥ 3 burrow openings to minimize trap saturation. Two intensive trapping sessions were conducted twice each year for the purpose of density estimation: one in early spring after emergence from hibernation, and the other during late July prior to adult females entering hibernation. During these sessions, populations were trapped for 3 to 4 consecutive days three times per day at 1.5-h intervals beginning at 0700. Population estimates and standard errors of the estimate were calculated using a closed population mark-recapture heterogeneity model (jackknife) (Pollock et al. 1990) from program CAPTURE (Otis et al. 1978) as recommended by Menkens and Anderson (1988) and Boulanger and Krebs (1994). At other times of the year, all experimental populations and controls A and D were trapped on a bi-weekly schedule for 1 day. Traps were then checked twice per day at 1-1.5-h intervals beginning at 0800.

At each capture, the squirrel was removed from the trap into a netted bag and marked in both ears with uniquely numbered metal eartags. At each capture I recorded eartag number, sex, weight, and reproductive status. Females were recorded as lactating (nipples large, dark, and secreting milk) or not lactating (nipples pink and small or dark and dried). Natal burrows were located either by observation (females carrying dry grass into cryptic holes during late May - early June) or by locating radio-collared females (Model PD-2C, Holohil Systems Ltd., Carp, Ontario, Canada) via radio-telemetry at midnight when squirrels are inactive and residing with their young.

I divided females into three reproductive classes that represent decreasing levels of energy expenditure to reproduction. If juveniles emerged from the female's natal chamber, she was classified as having "weaned" her young. If juveniles were never seen to emerge from the natal chamber but the female was recorded as lactating earlier in the season then she was classified as "failed" (i.e. entire litter died between parturition and weaning). If a female never lactated during the season, she was classified as "non-reproductive". This category included females that did not mate and those who may have aborted or resorbed their litter prior to parturition. Non-reproductive females were assumed to have the lowest energetic expenditure.

Litter size was not used as a measurement of reproductive investment or success during this study. Juveniles typically remain close to the natal burrow for the first week (Lacey 1991) unless the mothers move their young immediately upon emergence to an adjacent burrow system (McLean 1981). However, in some cases, adult females share burrow systems or live in close proximity with other adult females and mixing of juveniles among litters can occur even before emergence (Lacey 1991). Thus, I was not confident that juveniles could be assigned to a particular female in some cases. Although a litter could be assigned to an individual female in many cases, I did not limit my analyses to these females since doing so would bias the sample to females that lived distantly from others and experienced less competition for resources. Furthermore, litter size in arctic ground squirrels was only modestly affected by food resources (Hubbs and Boonstra 1997; Karels et al. 2000) and was highly variable and independent of population density (Chapter 2).

Reproductive parameters

Factors associated with the probability of a female lactating (i.e. having given birth) were analyzed using logistic regression in program JMP-IN (SAS Institute Inc.

1997). I considered three variables as potentially being associated with a female's probability of lactating. These were:

(1) age (a) of female which was known from trapping records from 1990 to 1996 (Hubbs and Boonstra 1997; Karels et al. 2000). All squirrels ≥ 3 years (maximum was 5 years) of age in 1996 were pooled into the 3-year old category since squirrels ≥ 3 years old represented only 14% (N = 125) of spring breeding populations. Yearlings represented 51% and two-year olds represented 34% of the populations.

(2) body condition (c) (grams) was estimated as the residual mass from a regression of spring mass on zygomatic arch breadth (mm) since body mass alone is not good predictor of reproductive success in ground squirrels (Dobson and Michener 1995).

(3) population density (d) (squirrels per ha).

I used a backwards elimination stepwise model selection routine described by Christensen (1997) to determine the effects that have the greatest contribution to the explanatory power of the model. The model notation that I used follows that of Christensen (1997). For example, the model notation "ac,cd" refers to a model that contains the interaction terms age*condition and condition*density plus all nested main effects age, condition, and density. A model with notation "ac,d" differs from the previous model in that there is no condition*density interaction term. Henceforth, "*" will be used for only describing single interactive effects.

The model selection method I used tests each term separately and sequentially beginning with higher order terms to determine which terms can be dropped from the initial model without the loss of explanatory power. The highest order term in the initial saturated model (all possible terms) is (a*c*d) and its effect on the explanatory power of the model is tested by removing it from the model and comparing the fit of the resulting model (ac, ad, cd), estimated by maximum likelihood, with that of the of the saturated model (acd) by a likelihood ratio test (G^2) (Christensen 1997). If the three-factor effect when removed does not significantly reduce the fit of the model to the data, then it can be safely removed without loss of explanatory power. Once the three-factor effect is removed, then the second step is to test each of the two-factor effects (a*c, a*d, c*d) separately against the reduced model (ac, ad, cd). Only the term with the highest associated *P*-value is removed. This procedure continues removing effects one at a time from the model until all remaining terms show a significant influence on the fit of the model. The steps for this analysis are shown in Table 3.2. Estimated odds ratios and 95% confidence limits for each parameter were calculated using equations in Hosmer and Lemeshow (1989).

Factors associated with the probability of a female weaning her litter (i.e. age, condition, and density) after she had given birth were analyzed using the same procedure as for the probability of lactating with one exception. Condition was estimated from the residuals of mass at parturition regressed on zygomatic arch breadth.

Survival parameters

I separated survival into two intervals, prehibernation and overwinter. Prehibernation survival was measured over an interval of 6 weeks from the date of juvenile emergence in the population (≈ 15 June in 1996) until the end of July. Female squirrels that disappeared during this interval and never recaptured were assumed to have died since female arctic ground squirrels are extremely philopatric (juveniles, Byrom and Krebs 2000; adults, Chapter 2). For overwinter survival, squirrels that were captured in

August and never recaptured during the next spring were assumed to have died. When fates were monitored by radio-telemetry, Karels et al. (2000) found that death during hibernation accounted for 94% of disappearances between August and the first spring trapping while 6% could be attributed to predation shortly before immergence or shortly after emergence from hibernation. Squirrels were assigned a dichotomous survival outcome variable (0 = survived time period, 1 = disappeared and assumed dead).

Factors associated with the probability of dying in each time period were analyzed with a similar procedure to that described for analyzing the probability of lactating. I used the same three variables measured at time of weaning for both prehibernation and overwinter survival: age (a); condition (c) as determined from residuals of body mass during late June (rather than spring mass) regressed on zygomatic arch; and density (d). I used an additional variable, reproductive status (r) (non-reproductive, failed, and weaned) to test for effects of reproduction on the probability of survival. I did not include age in the initial saturated model because sample sizes (prehibernation survival N = 67, overwinter survival N = 46) were too small to estimate the 22 parameters that would have resulted from its inclusion in the saturated models. I included density, condition, and reproductive status in the saturated models for backward elimination to determine the best model from these variables for each survival interval. I entered age and its possible interactions to the previous best model in a forwards stepwise approach (Christensen 1997). This method differs from the backwards approach in that the procedure begins with adding the main effect and testing if it significantly ($\alpha = 0.05$) improves the fit of the preceding model. If so, then more complex interactive effects are added and tested against the model from the proceeding step to determine which significantly improve the fit of the preceding model. The number of samples in each reproductive category changed with population density and no females at the highest density site weaned a litter and thus a survival probability could not be directly estimated for that combination. Hence, log-linear models were fit using the Newton-Raphson algorithm which can fit models to data when a combinations of factors are not present (Christensen 1997).

Prior to conducting logistic regression analyses, combinations of variables were examined for collinearity. No correlations were greater than Tabachnick's and Fidell's (1996) conservative criteria of $r = 0.70$ for exclusion of variables. All other statistical tests were performed according to procedures in Sokal and Rohlf (1995). Prior to the ANCOVA, Kolmogorov-Smirnov tests for normality and F-tests for equality of variances were performed using StatView (SAS Institute Inc. 1998). Kolmogorov-Smirnov tests for normality were also performed prior to linear regression. All continuous variables satisfied these criteria. Linear regression and ANCOVA were performed with SuperANOVA (Gagnon et al. 1991). All means are expressed as ± 1 S.E. except where stated and binomial confidence limits were calculated using program Ecological Methodology (Krebs 1998).

Results

Reproduction

Probability of lactation in arctic ground squirrels (N = 125) was dependent on population density and spring body condition but was independent of age (Table 3.2). Probability of weaning a litter by a female ground squirrel (N = 58) was dependent on population density (Table 3.3) but was independent of both age and condition at parturition. Odds ratios in Table 3.4 show the magnitude of effect for each variable predicting lactating or weaning. For the effect of density on the probability of not lactating, the odds ratio of 1.08 indicated that the probability of a female not lactating (i.e. not breeding or losing litter *in utero*) increased by a factor of 1.08 (8%) for every additional adult squirrel per ha in the population (Figure 3.2a). Furthermore, the odds of a female not lactating changed by a factor of 0.99 (-1%) for every gram increase in body condition. For example, a squirrel with a residual mass of +60g was 0.82 times (0.99^{20}) as likely to lactate (or 18% lower probability of lactating) than was a female with a residual mass of +80g.

Once a female had given birth, the probability that she would successfully wean her litter declined with population density (Figure 3.2b). The odds of a female failing to wean her litter changed by a factor of 1.26 for every additional squirrel per ha in the population (Table 3.4b). Figure 3.2c illustrates the realized reproduction of adult squirrels at the start of the breeding season by combining the probabilities of lactating and the probabilities of weaning a litter.

Model classification success

I assessed the success of the selected models for predicting lactation and weaning by applying the logistic equations using the parameters listed in Table 3.4 that were derived from squirrels in 1996 to squirrels with known reproductive fates in 1997. The logistic equation for lactation correctly classified 79% (N = 92) of the squirrels in 1997. The frequency of correct classification was a further 25% greater than if assignment had been random. However, classification was based on a cutoff value of 0.5. That is, any animal that scored a probability greater than 0.5 was classified as lactating, the rest were classified as non-lactating. However, the equations were better at correctly classifying lactating females (98% correct, N = 60) than at correctly classifying non-lactating females (44% correct, N = 32). However, since each individual animal is assigned a probability of lactating the cutoff chosen to assign that animal to either category is critical (Tabachnick and Fidell 1996). As long as the frequency of correct classification remains better than random assignment, cutoff values other than 0.5 will better determine the success of the model to discriminate among categories while minimizing Type I and Type II errors. Figure 3.3 shows the percentage of classifications that were correct when the cutoff value is increased. For predicting lactation, the percentage of correct classifications increased to 84% when the cutoff was 0.62, which was a 30% greater success than with random assignment.

The equations predicting weaning success based on 1996 data were poor predictors of weaning success of ground squirrels in 1997 at a cutoff of 0.5. Only 50% (N = 38) were correctly classified which was 3% less than if assignment had been random. However, with a cutoff value of 0.78, 87% of ground squirrels were correctly classified (Figure 3.3).

I combined the predicted probabilities of lactating with those of weaning to assess the model success for predicting the realized reproduction of the population. Overall, 77% (N = 69) of the female population were correctly classified to their known reproductive fate which was 15% greater than had assignment been random. All females who had weaned litters (N = 18) and 69% (N = 51) of those who did not wean litters

Table 3.2 Backward elimination stepwise logistic regression model selection for lactation in arctic ground squirrels. Variables age (a), condition (c) (residuals of spring body mass on structural size), and population density (d) were included in the saturated model (all interactions and main effects).

Step	Model	Deleted term	df	Log-Likelihood	G^2	R^2	Δdf	P
	Constant†	all	124	74.12				
1.	Saturated†	-	117	55.91	36.42	0.25	7	< 0.01
2.	ac,ad,cd†	a*c*d	118	56.79	1.76	0.23	1	0.18
3.	ad,cd	a*c	119	57.17	2.52	0.23	1	0.11
	ac,cd†	a*d	119	56.80	0.02	0.23	1	0.89
	ac,ad	c*d	119	56.86	0.14	0.23	1	0.71
4.	d,ac†	c*d	120	56.87	0.14	0.23	1	0.71
	a,cd	a*c	120	57.19	0.78	0.23	1	0.38
5.	a,c,d†	a*c	121	57.32	0.90	0.23	1	0.34
	ac	d	121	66.19	18.00	0.14	1	< 0.01
6.	d,c††	a	122	57.70	1.02	0.22	1	0.31
	a,d	c	122	63.74	13.10	0.14	1	< 0.01
	a,c	d	122	66.19	17.74	0.11	1	< 0.01
7.	c	d	123	66.87	18.34	0.10	1	< 0.01
	d	c	123	64.01	12.62	0.14	1	< 0.01

Note: Model notation refers to interactions plus main effects (e.g. ac,cd includes age*condition interaction, condition*density interaction, and the main effects of age, mass, and density). Each step lists (1) the model being tested, (2) the term deleted from the selected model from the previous step (marked with a '†'), (3) the total degrees of freedom in the model, (4) the log-likelihood value for the model, (5) the likelihood ratio test statistic of model with and without the term, (6) total variation explained by model, (7) the difference in degrees of freedom between the model with and without the term, and (8) the *P* values of the likelihood ratio test statistic. The most appropriate model selected by the procedure is marked with '††'.

Table 3.3 Backward elimination stepwise logistic regression model selection for weaning in arctic ground squirrels. Variables age (a), condition (c) (residuals of spring body mass on structural size), and population density (d) were included in the saturated model.

Step	Model	Deleted term	df	Log-Likelihood	G^2	R^2	Δdf	*P*
	Constant	all	57	40.06				
1.	Saturated†	-	50	20.04	40.04	0.50	7	<0.01
2.	ac,ad,cd†	a*c*d	51	20.04	0.00	0.50	1	1.00
3.	ad,cd	a*c	52	21.91	3.74	0.45	1	0.05
	ac,cd†	a*d	52	20.19	0.30	0.50	1	0.58
	ac,ad	c*d	52	21.06	2.04	0.47	1	0.15
4.	d,ac†	c*d	53	21.07	1.76	0.47	1	0.18
	a,cd	a*c	53	21.93	3.48	0.45	1	0.06
5.	a,c,d†	a*c	54	22.56	2.98	0.44	1	0.08
	ac	d	54	36.5	30.86	0.09	1	0.00
6.	a,c	d	55	38.99	32.86	0.03	1	<0.01
	c,d	a	55	22.91	0.70	0.43	1	0.40
	a,d†	c	55	22.61	0.10	0.44	1	0.75
7.	a	d	56	40.01	34.80	0.00	1	<0.01
	d††	a	56	22.97	0.72	0.43	1	0.40

Note: Model notation refers to interactions plus main effects (e.g. ac,cd includes age*condition interaction, condition*density interaction, and the main effects of age, mass, and density). Each step lists (1) the model being tested, (2) the term deleted from the selected model from the previous step (marked with a '†'), (3) the total degrees of freedom in the model, (4) the log-likelihood value for the model, (5) the likelihood ratio test statistic of model with and without the term, (6) total variation explained by model, (7) the difference in degrees of freedom between the model with and without the term, and (8) the *P* values of the likelihood ratio test statistic. The most appropriate model selected by the procedure is marked with '††'.

Table 3.4 Estimated odds ratios and 95% confidence limits for estimated logistic regression parameters. The odds ratios for density are increases in probability of a female ground squirrel (a) not lactating or (b) not weaning her litter for every increase of 1 squirrel per ha. The odds ratios for condition (residuals of spring body mass on structural size) are the increase in probability of a female not lactating for every increase of 1-g body condition.

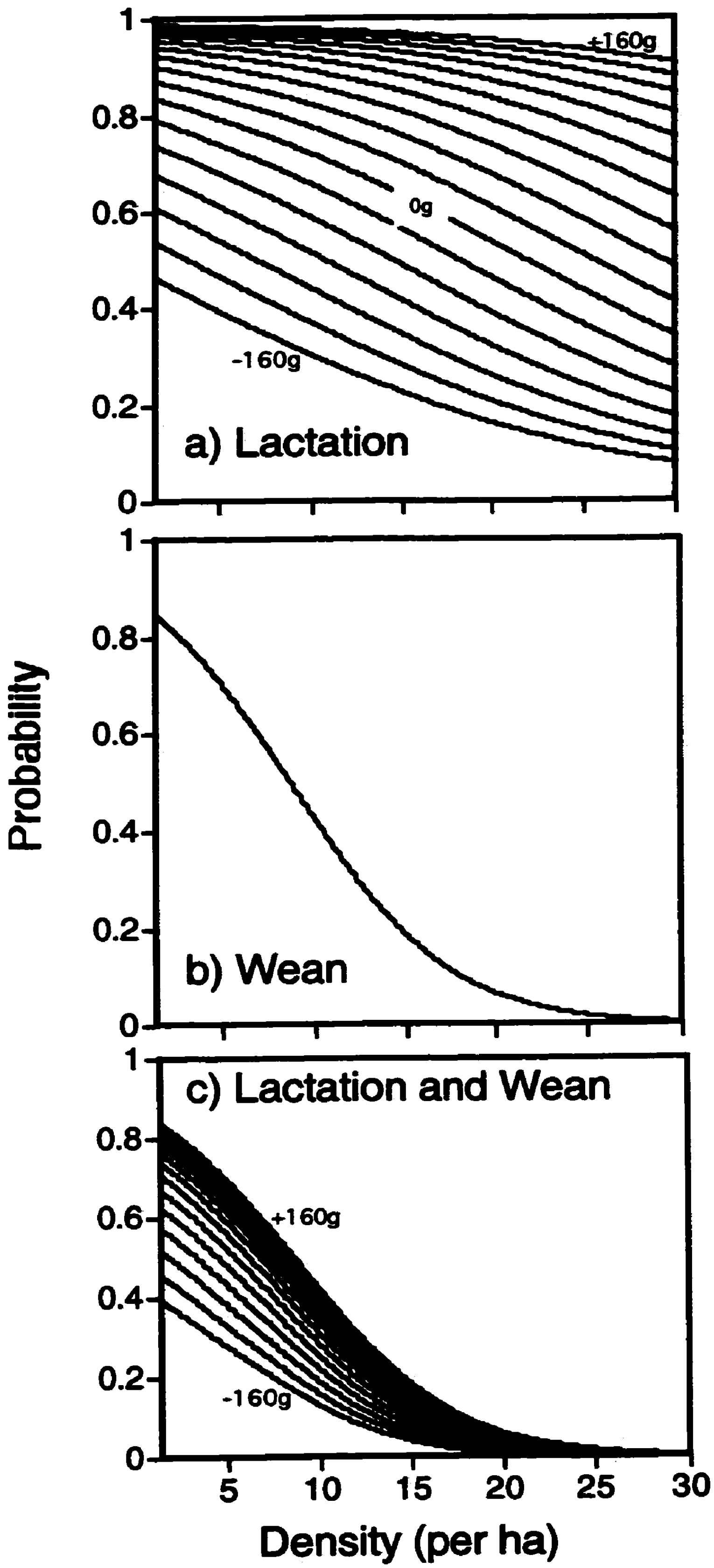
(a) Non-reproductive

Term	Parameter	S.E.	Odds Ratio	95% C.L.
Intercept	-2.33	0.42	0.10	0.04-0.22
Density	0.08	0.02	1.08	1.04-1.13
Condition	-0.01	0.00	0.99	0.98-1.00

(b) Failing to Wean Litter

Term	Parameter	S.E.	Odds Ratio	95% C.L.
Intercept	-2.10	0.62	0.12	0.04-0.41
Density	0.23	0.08	1.26	1.09-1.47

Figure 3.2 Probability of adult female arctic ground squirrel a) giving birth as deduced from lactation as a function of population density and body condition of 20g increments from -160g to + 160g residual spring body mass, and b) weaning a litter (for those who gave birth) as a function of population density. Probabilities were calculated from logistic regression equations with parameters from Table 3.4. The product of these probabilities are shown in c) the probability from spring emergence of a female successfully weaning a litter.


Probability
1
0.8
0.6
0.4
0.2
0
+160g
0g
-160g
a) Lactation
b) Wean
c) Lactation and Wean
+160g
-160g
5
10
15
20
25
30
Density (per ha)

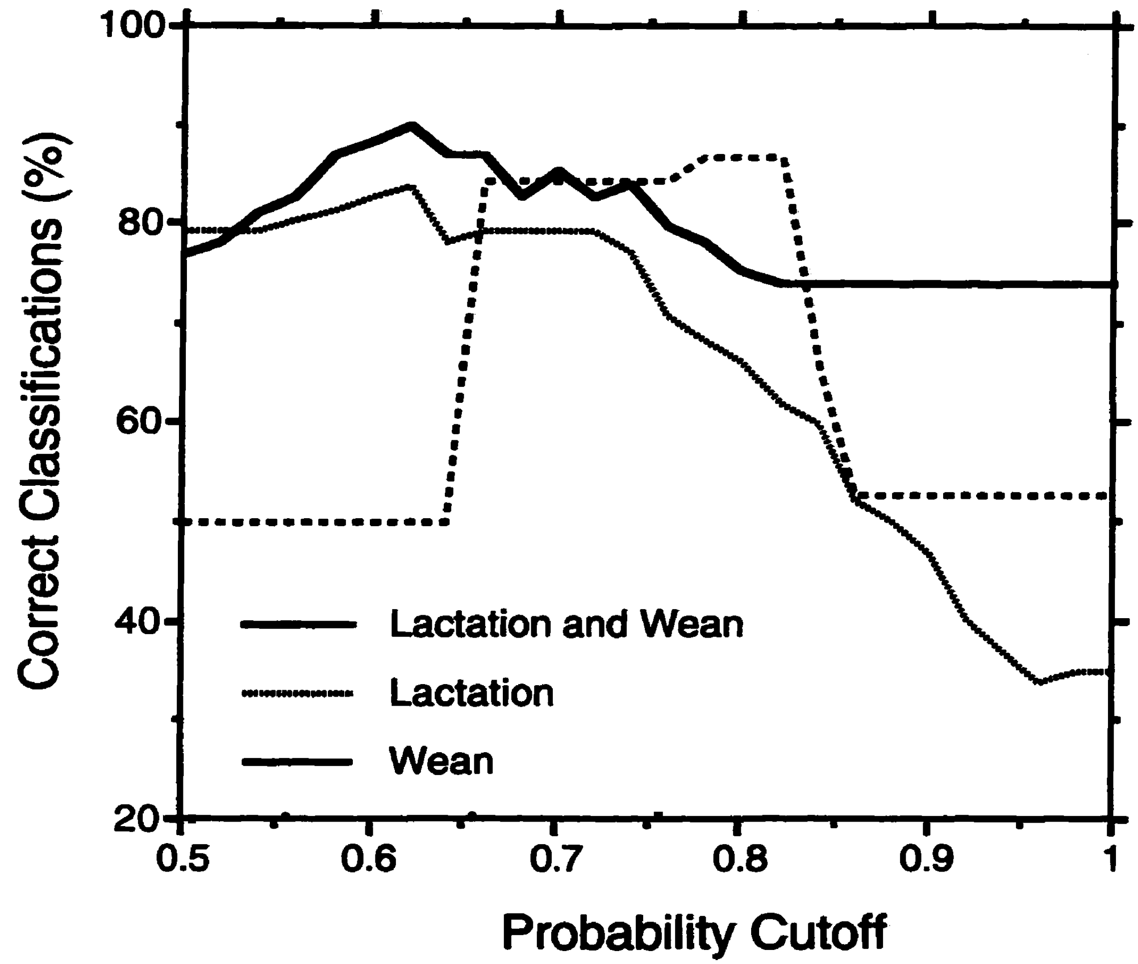


Figure 3.3 Percentage of female arctic ground squirrels correctly classified as lactating, successfully weaning a litter, or both during 1997 as a function of the probability cutoff for classification. Predicted probability was calculated from logistic equations based on data from 1996 in Table 3.4 and a probability was assigned to individual squirrels in 1997. The logistic models were considered successful predictors if the percentage of correct classifications were greater than had assignment been random. For lactating, weaning, and combined, the percentage of correct classifications assigned randomly was 55%, 53%, and 62% respectively.

(non-reproductive or failed) were correctly classified. With a cutoff value of 0.62, 90% were correctly classified (Figure 3.3).

Survival

Female adult survival (N = 67) from late June (when litters were weaned) until mid- to late August (hibernation) was dependent on both population density and on reproductive status (each operating independently) but independent of body condition at late June (Table 3.5; Figure 3.4). Age of the female as an independent variable significantly improved the fit of the logistic regression model (Table 3.5). Therefore survival was dependent on density, reproductive status, and age of the female. The odds of not surviving the summer changed by a factor of 0.90 (Table 3.6a) for every additional squirrel per ha (i.e. survival improved by 11% per additional squirrel per ha), and hence survival was inversely density dependent. Squirrels that were 2 and 3 years old were more than 2 and 5 times more likely to die by fall, respectively than were yearlings (Table 3.6a). The odds ratios for reproductive status (Table 3.6a) show that non-reproductive squirrels and squirrels that failed to wean litters were 1.2 and 3.4 times more likely to die by fall, respectively than were squirrels that successfully weaned litters.

Model selection for overwinter survival was complicated by the small sample size of females that survived to the end of summer (N = 46) and the extremely low overwinter survival of females that failed during lactation (7%, N = 14) and females that were non-reproductive (17%, N = 18). Overwinter survival of females that weaned young was 71% (N = 14).

Table 3.5 Backward elimination stepwise logistic regression model selection for survival of adult female arctic ground squirrels between the time litters are weaned and entry into hibernation. Variables reproductive class (r): non-reproductive, failed, or weaned; condition (c) (residuals of mass at weaning on structural size); and population density (d) were included in the saturated model. Age (a), was not included into the saturated model because of insufficient sample size for the number of parameters being estimated. Therefore age and possible interactions with age were tested separately by adding effects to the previously selected model marked (††).

Step	Model	Deleted term	df	Log-Likelihood	G^2	R^2	Δdf	P
	Constant†	all	66	41.66				
1.	Saturated †	-	55	35.62	12.08	0.14	11	0.36
2.	dc,dr,cr†	d*c*r	57	35.99	0.74	0.14	2	0.69
3.	dc,dr	c*r	59	36.04	0.10	0.14	2	0.95
	dc,cr†	d*r	59	36.02	0.06	0.14	2	0.97
	dr,cr	d*c	58	36.02	0.06	0.19	1	0.81
4.	r,dc†	c*r	61	36.05	0.06	0.13	2	0.97
	d,cr	d*c	60	36.04	0.04	0.14	1	0.84
5.	d,c,r†	d*c	62	36.05	0.00	0.13	1	1.00
	dc	r	63	39.10	6.10	0.06	2	0.05
6.	d,c	r	64	39.29	6.48	0.06	2	0.04
	d,r††	c	63	36.42	0.74	0.13	1	0.39
	c,r	d	63	38.48	4.86	0.08	1	0.03
7.	d	r	65	39.78	6.72	0.05	2	0.03
	r	d	64	39.80	6.76	0.04	1	0.01

Testing for age effects

Step	Model	Added term	df	Log-Likelihood	G^2	R^2	Δdf	P
1.	d,r,a††	a	62	34.45	3.94	0.17	1	<0.05
2.	d,ra	r*a	60	34.02	0.86	0.18	2	0.65
	da,r	d*a	61	33.55	1.80	0.19	1	0.18

Note: Model notation refers to interactions plus main effects (e.g. ac,cd includes age*condition interaction, condition*density interaction, and the main effects of age, mass, and density). Each step lists (1) the model being tested, (2) the term deleted from the selected model from the previous step (marked with a '†'), (3) the total degrees of freedom in the model, (4) the log-likelihood value for the model, (5) the likelihood ratio test statistic of model with and without the term, (6) total variation explained by model, (7) the difference in degrees of freedom between the model with and without the term, and (8) the *P* values of the likelihood ratio test statistic. The most appropriate model selected by the procedure is marked with '††'.

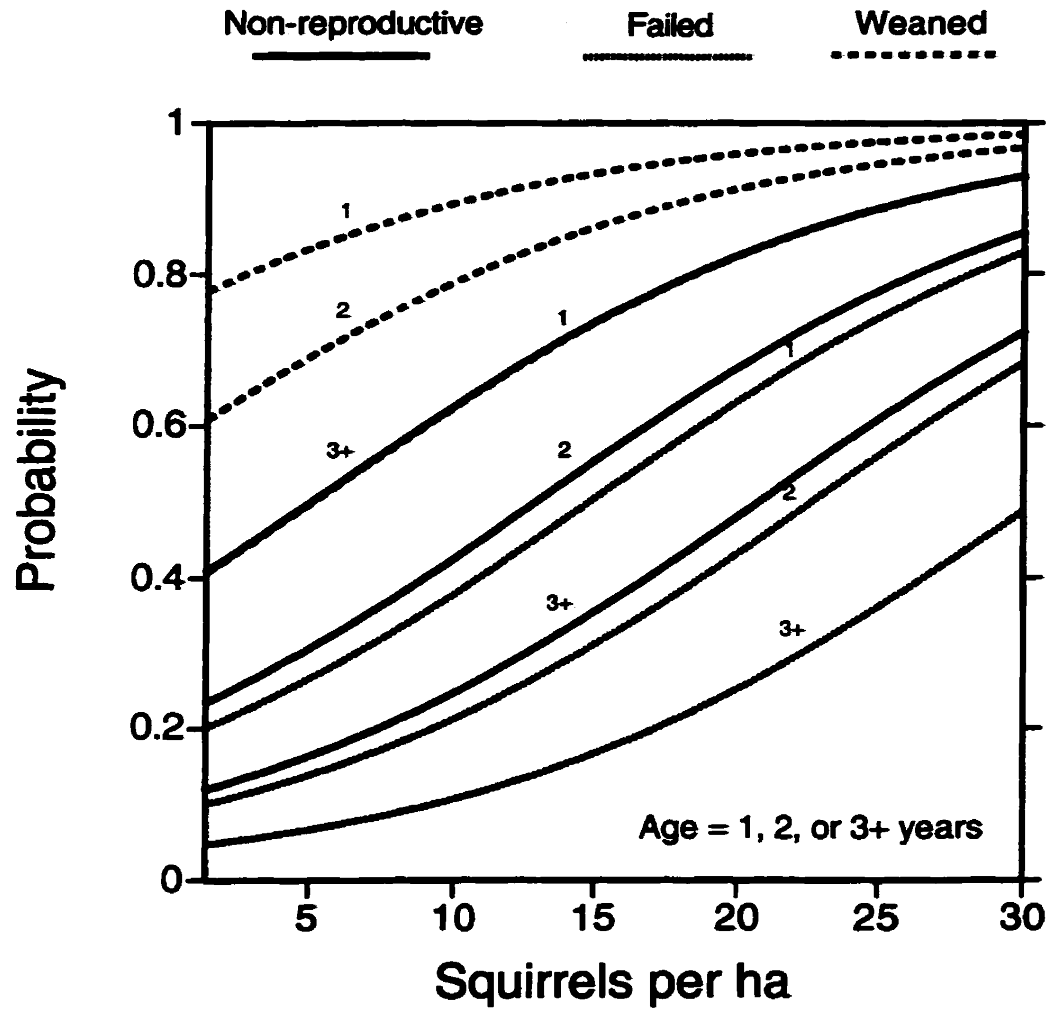


Figure 3.4 Probability of survival from late June (weaning period) until entry into hibernation for female arctic ground squirrels over increasing population densities. Ground squirrels were classified as ages 1, 2, or ≥ 3 years and as non-reproductive, litter failed during lactation, and successfully weaned litter. The survival curve for females 3+ years old who weaned a litter is hidden underneath the survival curve for non-reproductive females (age = 1).

Table 3.6 Estimated odds ratios and 95% confidence limits for estimated logistic regression parameters. The odds ratios are the increase in probability of a female ground squirrel (a) not surviving the summer or (b) not surviving overwinter for every unit increase in the term. For reproduction terms (non-reproductive and failed), the odds ratios are the increase in probability of not surviving relative to a female who was able to wean her young.

(a) Pre-hibernation mortality

Term	Parameter	S.E.	Odds Ratio	95% C.L.
Intercept	-0.49	0.82	0.61	0.12-3.06
Density	-0.10	0.04	0.90	0.84-0.97
Reproduction (non-reproductive)	0.20	0.52	1.23	0.44-3.42
Reproduction (failed)	1.21	0.49	3.36	1.37-8.47
Age	0.81	0.42	2.26	0.99-5.16

(b) Overwinter mortality

Term	Parameter	S.E.	Odds Ratio	95% C.L.
Intercept	1.57	77.63	4.79	-
Age	1.89	1.06	6.6	0.83-52.70
Condition	0.01	0.01	1.01	0.99-1.04
Density	0.02	2.58	1.02	0.01-160
Reproduction (non-reproductive)	-4.94	77.61	0.01	-
Reproduction (failed)	12.4	155.2	243643	-
Density*Reproduction (non-reproductive)	0.14	2.58	1.15	0.01-180
Density*Reproduction (failed)	-0.42	5.16	0.65	0.00-16048

When categories are occupied by too few samples the data are likely to be overdispersed, and therefore low power of the analysis is expected (Christensen 1997). In these situations the fit becomes perfect which causes the slope of the logistic equation to approach infinity (Sall and Lehman 1996). However, because parameter estimates are handled through likelihood rather than theoretically infinite values, hypotheses can still be tested (Sall and Lehman 1996) even though standard errors and confidence limits can not be estimated. For small samples sizes, the sampling distribution of the odds ratio tends to be skewed to the right from being bounded away from zero and will approach normality only when sample sizes are large and beyond that of most studies (Hosmer and Lemeshow 1989); hence the high upper 95% confidence limits for most terms in Table 3.6. However, the sampling distribution associated with the original parameter for each odds ratio approximates normality even with small sample sizes (Hosmer and Lemeshow 1989).

Table 3.7 shows the model selection routine for overwinter survival. Although I continued the procedure to step 7, which eliminates single factor terms, there was no support for selecting any of the subsequent models beyond step 4 since they were nearly equally poor (or equally good if power is low) based on *P*-values. I therefore selected the last model with all three variables (condition, density * reproductive status) that was known to contain at least one significant term (density * reproductive status). I added age both independently and interactively to the model, from which only the independent effect of age improved the fit of the model (Table 3.7). Therefore overwinter survival was dependent on age, condition, density, and reproductive status. However, age had independent effects on survival from the effects of condition and both terms were independent from an interactive effect on survival between density and reproductive status.

The probability of overwinter mortality increased by a factor of seven for each additional year of age and by a factor of 1.01 for every gram increase in condition at time of weaning (Figure 3.4; Table 3.6b). Mortality associated with reproductive status was complicated by an interaction with population density. Figure 3.5 illustrates the interactive effects of density and reproduction on the probability of overwinter survival for different condition classes (-55 g, 0, and + 55 g residual body mass at weaning) separated by age class. The figure illustrates four main points. First, most females that failed during lactation died overwinter (13 of 14). Second, for females that were non-reproductive or weaned litters, survival declined with increasing population density and age. Third, females that weaned their litters had a greater probability of survival than females that were non-reproductive when densities were less than 17 squirrels per ha. Fourth, when densities were above 17 per ha, non-reproductive females had the greatest probability of overwinter survival. This was associated with a large proportion of non-reproductive females in the population that was denser than 17 per ha. In 1996, 60% of adult female population on the highest density site (30.1 per ha) showed no signs of lactation (Figure 3.6). This was approximately 2 - 4 times the percentage of non-reproductive females (16 - 32%) in lower density populations (1.6-11.6 per ha)

Model classification success

The logistic models for prehibernation survival from weaning to fall derived from data in 1996 were able to correctly classify survival for 58% (N = 67) of females in 1997, which is 8% greater than had assignment been random. Nearly all (96%, N = 28) females that died were correctly classified while only 31% (N = 39) who survived were correctly classified. The overall maximum success of the model remained at 58% despite changes in the cutoff values (Figure 3.7).

The logistic models for overwinter survival derived from data in 1996 were able to correctly classify survival for 61% (N = 36) of the females in 1997 which was 11% greater than had assignment been random. Most (72%, N = 18) females that died were correctly classified and 50% (N = 18) who survived were correctly classified. The overall maximum success of the model remained at 61% despite changes in the cutoff values (Figure 3.7).

Mass and condition before hibernation

The mass of adult female ground squirrels just prior to hibernation was not dependent on population density (linear regression, $r^2 = 0.03$, df = 63, $P = 0.19$) however, body condition (residuals from fall body mass regressed on zygomatic arch) declined significantly with population density (linear regression, slope = -1.63, $r^2 = 0.08$, df = 60, $P = 0.03$). Therefore, I used density as a covariate in an ANCOVA to examine fall condition of females among the reproductive classes. Fall condition among the reproductive classes was ranked non-reproductive > failed > weaned, but differences were not significant (Table 3.8). The mean difference in fall condition (2.5g) between those who survived and those who died overwinter was also not significant (Table 3.9). Therefore, there was no evidence that the effects of reproductive status and population density influence overwinter survival through changes in body condition prior to entry into hibernation.

Future reproduction

To determine if there were any costs of reproduction on future fecundity, I examined the reproduction of squirrels in 1997 that had survived from 1996 to 1997 by comparing those that weaned litters in 1996 with those that were non-reproductive in 1996. Females who failed during lactation were not examined because only one of 25 survived from 1996 to 1997. There was no evidence that reproduction in 1996 compromised reproduction in 1997. For those females that weaned a litter in 1996 and survived to the next season, 91% (10 of 11) gave birth the following season, one of which later failed during lactation. Thus 90% (9 of 10) of the females that successfully weaned a litter in 1996 also weaned a litter the following season. For those females that were non-reproductive in 1996, 80% (4 of 5) gave birth in 1997. Weaning rates were unknown for those females.

Table 3.7 Backward elimination stepwise logistic regression model selection for overwinter survival in arctic ground squirrels. Variables reproductive class (r): non-reproductive, failed, or weaned; condition (c) (residuals of spring body mass on structural size); and population density (d) were included in the saturated model. Age (a), was not included in the saturated model because of insufficient sample size for the number of parameters being estimated. Therefore age and possible interactions with age were tested separately by adding effects to the previously selected model marked (††) at step 4.

Step	Model	Deleted term	df	Log-Likelihood	G^2	R^2	Δdf	*P*
	Constant†	all	45	28.27				
1.	Saturated†	-	34	17.02	22.50	0.40	11	0.02
2.	dc,dr,cr†	d*c*r	36	17.94	1.84	0.37	2	0.40
3.	dc,dr†	c*r	38	18.10	0.32	0.36	2	0.85
	dc,cr	d*r	38	18.50	1.12	0.35	2	0.57
	dr,cr	d*c	37	18.24	0.60	0.35	1	0.44
4.	r,dc	d*r	40	18.90	33.80	0.33	2	<0.01
	c,dr††	d*c	39	18.42	0.64	0.35	1	0.42
5.	c,d,r†	d*r	41	19.30	1.76	0.32	2	0.41
	dr	c	40	18.65	0.46	0.34	1	0.50
6.	d,r†	d*r	42	19.44	0.28	0.31	1	0.60
7.	d†	r	44	20.72	2.56	0.27	2	0.28
	r	d	43	20.09	1.30	0.29	1	0.25

Testing for age effects

Step	Model	Added term	df	Log-Likelihood	G^2	R^2	Δdf	*P*
1.	c,dr,a††	a	38	15.91	5.02	0.44	1	0.03
2.	ca,dr	m*a	37	15.26	1.2	0.46	1	0.46
	c,dr,da	d*a	37	15.49	2.64	0.48	1	0.48

Note: Model notation refers to interactions plus main effects (e.g. ac,cd includes age*condition interaction, condition*density interaction, and the main effects of age, mass, and density). Each step lists (1) the model being tested, (2) the term deleted from the selected model from the previous step (marked with a '†'), (3) the total degrees of freedom in the model, (4) the log-likelihood value for the model, (5) the likelihood ratio test statistic of model with and without the term, (6) total variation explained by model, (7) the difference in degrees of freedom between the model with and without the term, and (8) the *P* values of the likelihood ratio test statistic. The most appropriate model selected by the procedure is marked with '††'.

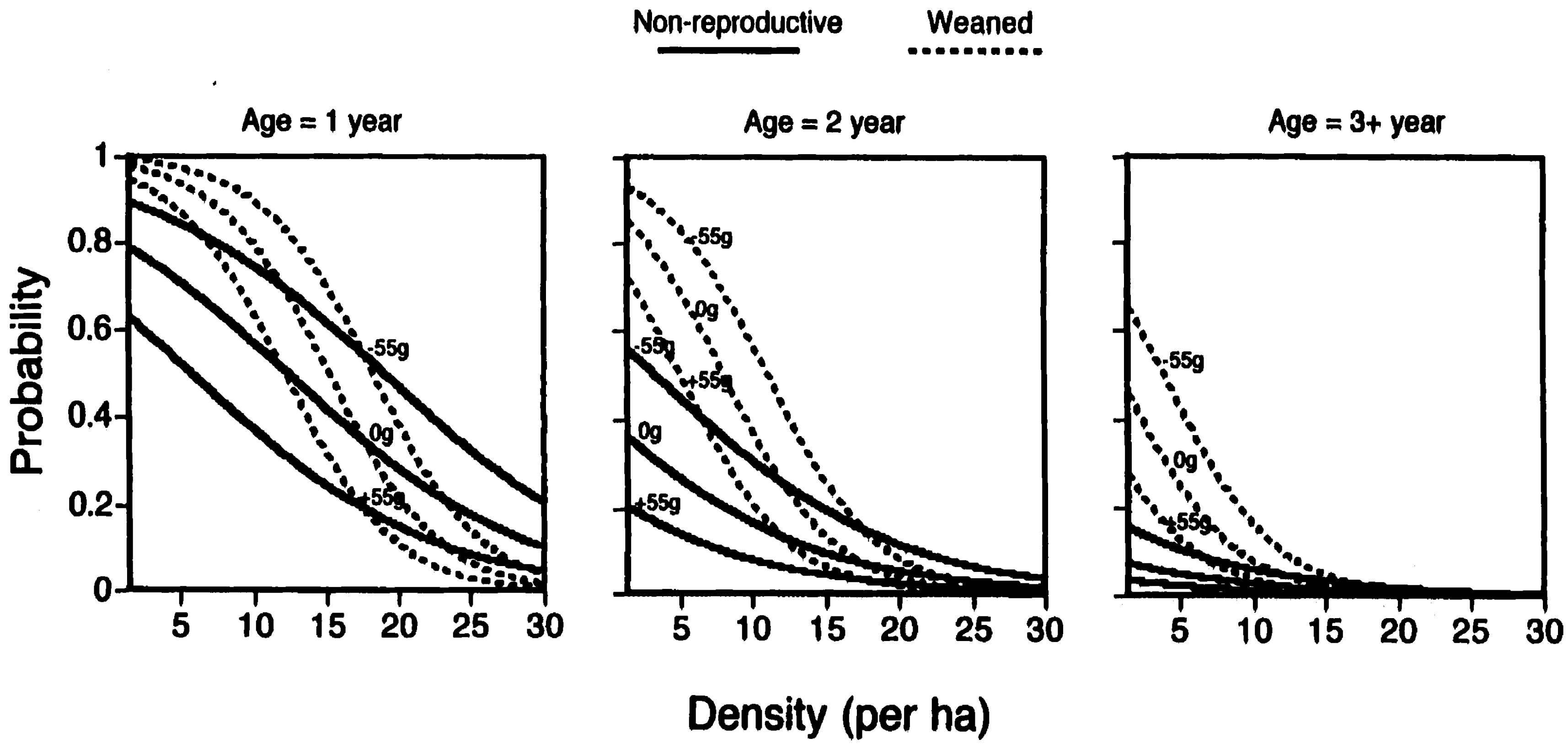


Figure 3.5 Probability of survival during hibernation for adult female arctic ground squirrels as a function of age, condition, and population density. Overwinter survival is complicated by an interaction between condition at weaning (residuals of body mass on zygomatic arch) and age and an interaction between population density and reproductive status (non-reproductive, failed during lactation, weaned litter). Therefore, plots are separated by age of the squirrel and survival is plotted for squirrels of condition of 0g ± 1 standard deviation (55g) for each reproductive status. Survival curves of females who failed during lactation do not appear on the figures owing to nearly complete mortality (13 of 14).

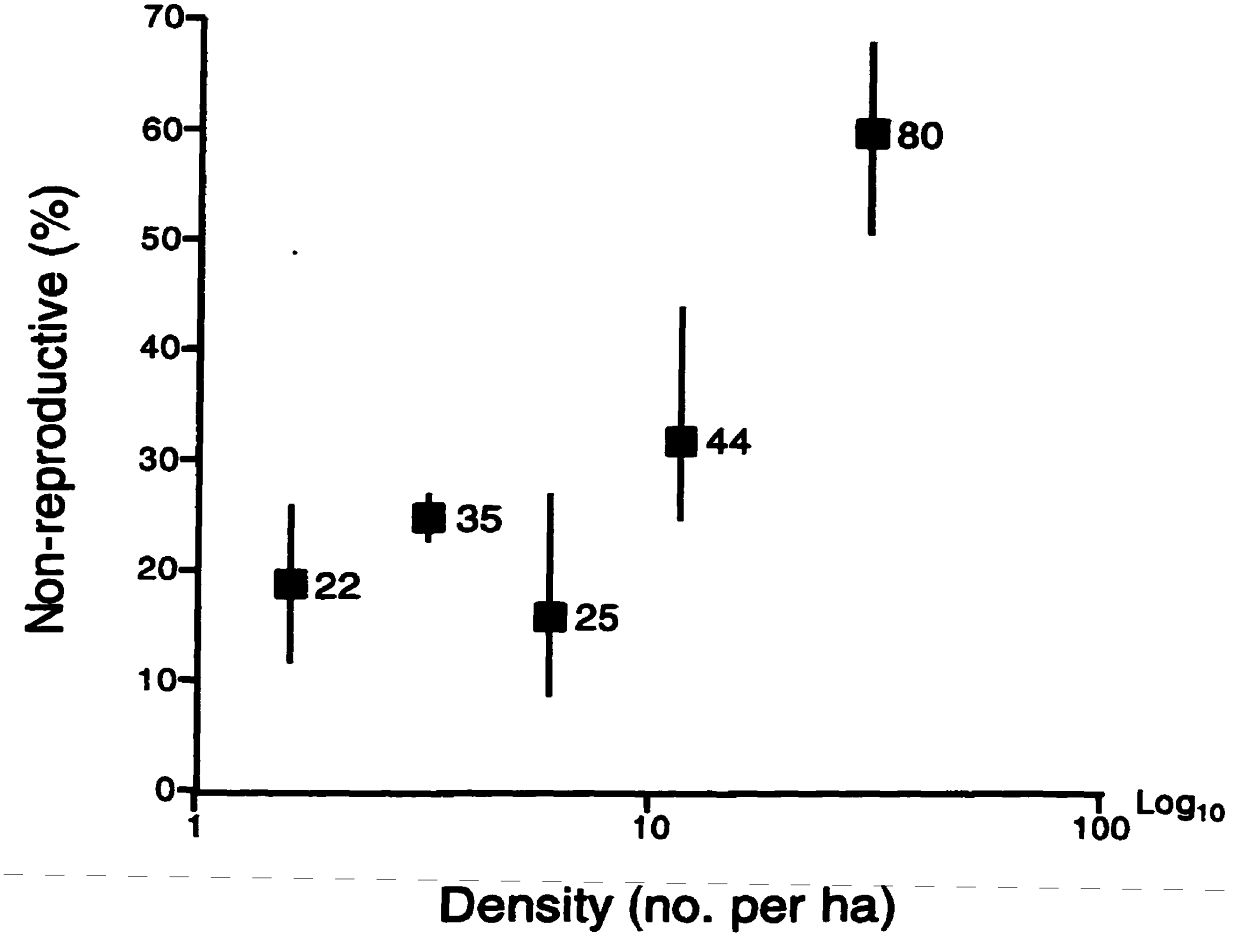


Figure 3.6 Percentage of female arctic ground squirrels that never gave birth during 1996 in each population. The percentage of non-reproductive females in the highest density site was 2 - 4 times that of the rest of the sites. 95% confidence limits and sample sizes are shown.

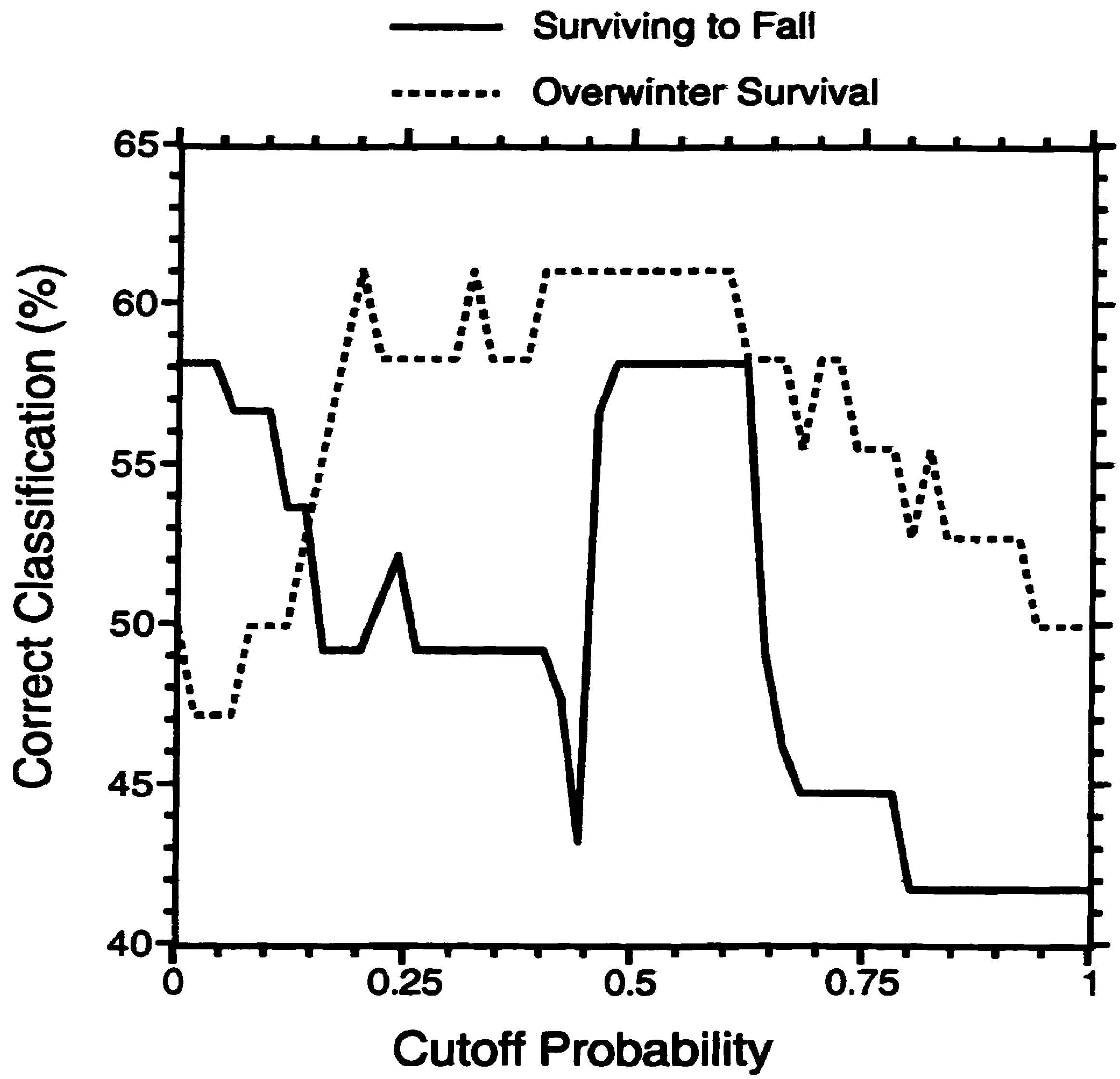


Figure 3.7 Percentage of female arctic ground squirrels in 1997 correctly classified as surviving to fall or surviving overwinter as a function of the probability cutoff for classification. Predicted probability was calculated from logistic equations based on data from 1996 in Table 3.5 and a probability was assigned to individual squirrels in 1997. The logistic models were considered successful predictors if the percentage of correct classifications was greater than had assignment been random. For survival to fall and overwinter survival, the percentage of correct classifications assigned randomly was 50% for both.

Table 3.8 Comparison of least squares mean of fall condition (residuals from fall body mass regressed on zygomatic arch) for adult female arctic ground squirrels in 1996 among three reproductive classes (weaned young, failed during lactation, and non-reproductive).

Reproductive Status	LS mean (g)	S.E.	N
Weaned	-131.9	51.8	21
Failed	10.5	15.9	19
Non-reproductive	50.3	21.2	22

one-way ANCOVA

Term	F	df	*P*
Reproductive Status	2.5	2	0.14
Covariate: Density	15.9	1	< 0.001
Density × Reproductive status	2.9	2	0.06

Table 3.9 Comparison of least squares mean of fall condition (residuals from fall body mass regressed on zygomatic arch) for adult female arctic ground squirrels who lived or died overwinter from 1996.

Overwinter Survival	LS mean (g)	S.E.	N
Yes	-8.6	19.3	21
No	-6.1	11.7	41

one-way ANCOVA

Term	F	df	*P*
Survival	2.0	1	0.16
Covariate: Density	5.5	1	< 0.02
Density × Survival	2.3	1	0.13

Discussion

Female arctic ground squirrels that were in better condition in the spring were mostly likely to give birth, however the probability of birth declined with increasing population density for all squirrels (Figure 3.2a). For those females who did give birth, the probability of weaning their litter declined with increasing population density (Figure 3.2b). There was no evidence of reproductive senescence as older females were as likely to give birth and wean their young as were younger females (Table 3.2, Table 3.3). Survival from late June (the time of weaning) until late August increased with increasing population density but was poorer for older animals where survival declined by more than half for every year of age (Figure 3.4). However, reproduction influenced survival such that females that had reproduced and weaned their litter had the highest survival (Figure 3.4). In comparison with females who successfully weaned their litter, females who were non-reproductive had 1.2 times poorer survival and females who failed to wean their litter had 3.4 times poorer survival. Both reproductive status and population density influenced overwinter survival. Overwinter survival generally declined with increasing population density but had a greater effect on females who successfully weaned their litter. Females that reproduced and weaned their litter had the highest survival except at high densities (> 17 per ha) when non-reproductive females had higher survival (Figure 3.5). Nearly all (93%, N = 14) females who gave birth and failed to wean their litter died over winter. Older animals were least likely to survive the winter, with survival decreasing by a factor of seven for every year of age.

Reproduction

Female adult ground squirrels had higher reproductive success with increasing maternal condition (measured by residuals of mass on zygomatic arch breadth) and decreasing population density (Figure 3.2c) but was independent of maternal age. Birth rates (as indicated by presence of lactation) declined as population density increased and as maternal condition declined. Weaning rates declined as population density increased but were independent of changes in maternal condition. The reproductive ability of females in many mammal species including ground squirrels has been demonstrated to be affected by physiological condition when measured by mass, changes in mass, or fat reserves influencing reproductive success [red deer (*Cervus elaphus*) Clutton-Brock et al. 1986; white footed mouse (*Peromyscus leucopus*) Morris 1992; cotton rats (*Sigmodon hispidus*) Campbell and Slade 1995; eg. water voles (*Arvicola terrestris*) Bazhan et al. 1996; Soay sheep *Ovis aries* Clutton-Brock et al. 1996; bighorn sheep (*Ovis canadensis*) Festa-Bianchet et al. 1998; alpine marmots (*Marmota marmota*) Hackländer and Arnold 1999; Richardon's ground squirrels (*S. richardsonii*) Dobson and Michener 1995; Uinta ground squirrels (*S. armatus*) Rieger 1996; Columbian ground squirrels (*S. columbianus*) Dobson and Kjelgaard 1985; Risch et al. 1995; Dobson et al. 1999] Therefore, condition-dependent reproductive success of arctic ground squirrels in my study is consistent with that of other mammal species.

The density-dependent decline in reproduction that I have shown occurs in other mammal species as well (reindeer (*Rangifer tarandus*) Skogland 1983; Skogland 1985; feral donkeys (*Equus asinus*) Choquenot 1991; red squirrels (*Sciurus vulgaris*) Wauters and Lens 1995; bighorn sheep Festa-Bianchet et al. 1998; water voles Koskela et al.

1999). Density-dependent reduction in reproduction also exists in other species of ground squirrels. For example, following a drought, Van Horne et al. (1997) found that in Townsend's ground squirrels (*S. townsendii*), high-density populations in sagebrush habitats had poorer reproductive success than low-density populations in grassland habitats. Dobson (1995), in an experiment similar to mine, showed that production of young in Columbian ground squirrels declined significantly after the cessation of a two-year food supplementation experiment at two sites at different elevations. However, production of young at these sites did not decline below that of an unmanipulated control population at each elevation. Both of these studies point to the importance of intraspecific competition for food resources influencing reproductive output.

Early spring body condition, as measured by residuals of mass on structural size, was important in the early stages of reproduction for female arctic ground squirrels. Fertility appears to be high in most years for arctic ground squirrels (≈ 80%) (Lacey et al. 1997; Karels et al. 2000), but it is not known if fertility responds to changes in environmental conditions. It is not clear when the decision is made to either terminate or sustain the pregnancy between emergence and parturition. In most years, mating was completed before I arrived at the study site at a time when the only cues available for squirrels to sustain pregnancy were population density and body condition. The effect that these cues have on squirrel reproduction could be simultaneous or sequential. Oestrus may be regulated by body condition at emergence since natural food availability cannot be assessed at this time. Density alone cannot be a cue for initial commitment to breed because approximately 88% of females will breed even at high densities (Karels et al. 2000) and in one year (1997) on a high-density food supplemented population, 94% of female arctic ground squirrels gave birth (Chapter 2) despite the fact that I was unable to supplement food to that population until 1-2 weeks after their spring emergence. Therefore it appears that females may abort or resorb their embryos later during gestation once intraspecific competition for spring vegetation begins. Whether or not resorption or abortion of embryos is adaptive or a consequence of nutritional stress is unknown for arctic ground squirrels. However, adaptive resorption is a possibility. Embryo resorption has been shown to occur in alpine marmots in order to maximize their long-term fitness (Hackländer and Arnold 1999).

Population density had a strong, negative effect on weaning success among arctic ground squirrel females that gave birth (Figure 3.2) but it is unclear why maternal condition at parturition was an unimportant factor. The importance of maternal body condition in permitting weaning of young has been shown in other mammalian studies (Clutton-Brock et al. 1986; McNamara 1995; Gerhart et al. 1997). In an earlier study, female arctic ground squirrels in better condition were more likely to wean young (Karels et al. 2000). However, in that study, non-reproductive females (i.e. those that never gave birth) were pooled with females who failed during lactation and hence that analysis on weaning rate included the effect of condition on birth rate. The index of condition that I used, which was a good predictor of pre-weaning reproduction (Dobson and Michener 1995), may not be a good predictor of the ability of females to wean litters, or it may be confounded by other pre-emergent juvenile mortality factors that mask the effects of maternal condition.

Pre-emergent young may have died owing to direct causes such as predation or infanticide. Possible predators of neonatal ground squirrels in my study area include grizzly bears (*Ursus arctos*) and weasels (*Mustela erminea* and *M. nivalis*). Grizzly bears have been reported to be important predators on arctic ground squirrels in tundra environments (Carl 1971), but predation by grizzly bears on ground squirrels in the boreal forest has not been detected in 8 years of investigation in my study area. Weasels are the only predator small enough to enter ground squirrel burrows, but they are too rare in my study area to account for the degree of variation of weaning rates among sites (see discussion in Karels et al. 2000). Only one suspected weasel kill has been recorded in my study area and that was of a post-emergent juvenile ground squirrel (Byrom and Krebs 1999). Also, weasels pose little threat to a litter in the presence of adult ground squirrels, since adult arctic ground squirrels chase weasels (Simpson 1990; pers. obs.) perhaps to protect juveniles. Infanticide by females has been reported in Columbian ground squirrels (Dobson 1990; Hare 1991) and in black-tailed prairie dogs (Hoogland 1995), but not in arctic ground squirrels. Infanticide in arctic ground squirrels is reported to be committed only by males (McLean 1983; Lacey 1991). Mclean (1983) found that infanticide was rare and that males killed mostly post-emergence juveniles. The infrequent occurrence of infanticide cannot account for the marked differences in weaning rate that I observed among sites.

Another explanation why entire litters failed during lactation may be directly related to females' diet during lactation, which may affect the quality or quantity of milk they provided to young. In a review of metabolism of adipose tissue and its role in lactation, McNamara (1995) attributed the variation in milk production among animals of similar body composition and genotype to changes in dietary fats which produces fluctuation in rates of glucose utilization in adipose tissue. For example, dietary studies on lactating cows and humans have shown that increasing the fatty acid content in diet quickly (< 6 hours in humans, Francois et al. 1998) alters the fatty acid composition, fat content, and quantity of milk (Schingoethe et al. 1996; Francois et al. 1998; Sauer et al. 1998; Chouinard et al. 1999). Offspring born to lactating female rats that are fed a diet deficient in essential fatty acids [i.e. those fatty acids obtained from plants that cannot be synthesized by vertebrates but are metabolically indispensable (Pond 1998)] grow more slowly and are more than four times less likely to survive to weaning compared with offspring from females on a control diet (Henry et al. 1996). It is unclear whether the high mortality rate of pre-weaned offspring is dependent on a reduction of milk output of the mother or a reduction in transfer of essential fatty acids. Dairy calves fed milk replacers deficient in essential fatty acids show increased red blood cell fragility (Jenkins and Kramer 1985). Furthermore, reviews of the dietary requirements of essential fatty acids during pregnancy and lactation stress the importance of essential fatty acids (α-linolenic acid) and their metabolic derivatives (docosahexaenoic acid) in brain and possibly retinal development in infants (Neuringer et al. 1988; Sanders 1999).

The hypothesis that arctic ground squirrels failed to wean litters because of a lack of essential fatty acids assumes that fatty acids are a potentially limiting resource in natural populations. The quantity of fatty acids in plants varies among species and tissue type (Florant et al. 1990; Hill and Florant 1999) and are rare in some environments (Pond 1998). However, there is no evidence to support the hypothesis that essential fatty acids can be limiting to natural populations. In contrast, there is strong evidence that arctic ground squirrel reproduction in the boreal forest is food limited since reproductive parameters, such as lactating rate, weaning rate, and litter size are improved when supplemented with food (commercial rabbit chow) that is nutritionally optimized for rabbits (Hubbs and Boonstra 1997; Karels et al. 2000, Chapter 2). Additionally, herbivory on preferred plant species by arctic ground squirrels during this study increased with population density and highly preferred species were completely eliminated from the plant community at high densities (Chapter 2). However, herbivory, as measured by standing crop biomass, was measured several weeks after squirrels would have weaned their young. Nevertheless, the intensity of herbivory on select plant species does provide evidence that strong competition for preferred plant species does occur. Strong competition would most likely have also occurred during the lactation period such that dietary requirements during lactation may not have been obtained at high density.

Prehibernation survival

Adult survival of female arctic ground squirrels between weaning and hibernation was dependent on previous reproductive status, on population density, and on age (Figure 3.4) but not on body condition at time of weaning. In contrast to the prediction from the cost of reproduction hypothesis that females weaning their litter would compromise their own survival, survival was greatest for females that weaned a litter. Although survival for females who did not give birth was only 20% less than that of successful females, females who failed during lactation were 3 times more likely to die than were successful females. Survival for all reproductive classes declined with age but independently increased with population density (Figure 3.4).

Predation is the ultimate cause of mortality for arctic ground squirrels in the boreal forest during their active period (Hubbs and Boonstra 1997; Byrom and Krebs 1999; Byrom et al. 2000), but may not be the proximate cause. Factors such as age and reproductive status may alter the susceptibility of squirrels to predation. The result that survival increased with population density suggests that predator detection may have been enhanced at high densities thus reducing the rate of mortality as has been found in suricates (*Suricata suricatta*) (Clutton-Brock et al. 1999). Condition at weaning was not important in predicting pre-hibernation survival; therefore it is unlikely that starvation was the proximal cause of mortality unless squirrels declined rapidly in condition after the weaning period. Ben-David et al. (1999) conducted a study of condition indices in arctic ground squirrels several weeks after the weaning period and concurrently with this study on the same sites. They found that in 20 females taken from a range of population densities, evidence of severe nutritional stress occurred in only one female that was living on a moderate density (5.9 per ha) site with natural food resources. They also showed that water was not limiting because females were not water-stressed despite the marked differences in population density.

Females who failed during lactation might have had a diet deficient in essential fatty acids owing to intraspecific competition and I propose that this deficiency may have also negatively affected survival. Hill and Florant (1999) measured fatty acid composition in free ranging yellow-bellied marmots and found that females were unable to increase the quantity of essential fatty acids (α-linolenic) in their adipose tissue during reproduction. Females that are deficient in essential fatty acids and that attempt reproduction may be unable to compensate for their deficiency until after lactation ceases. Therefore, they may still be deficient later in the season. Rodents fed a diet deficient in essential fatty acids show poorer protein retention efficiency and increases up to 30% in metabolic rate independent of temperature (Rafael et al. 1984; Rafael et al.

1988; Yazbeck et al. 1989; Henry et al. 1996). Henry et al. (1996) found that rats fed a diet deficient in essential fatty acids compensated for the negative effects by consuming more food. However, metabolic rates of normothermic (not in torpor) yellow-bellied marmots (Thorp et al. 1994) and deer mice (*Peromyscus maniculatus*) (Geiser 1991) are unaffected by changes in fatty acid content in their diet. If ground squirrels deficient in essential fatty acids increase their foraging rate to compensate for a higher metabolic demand, or to obtain the quantities of stored fatty acids necessary for efficient hibernation (Florant 1998), they may increase their vulnerability to predators and thus suffer higher rates of mortality.

Overwinter survival

Overwinter survival decreased with age but increased with declining condition which is opposite to what has been shown for Columbian ground squirrels (Murie and Boag 1984) and yellow-bellied marmots *Marmota flaviventris* (Lenihan and Van Vuren 1996) where body mass and condition are positively associated with increased overwinter survival. Reproductive status had a strong impact on overwinter survival, but it was complicated by an interaction with population density (Table 3.1, Figure 3.5). Nearly all females that failed during lactation died overwinter (13 of 14). The rate of overwinter survival for females that weaned litters declined with population density at a greater rate than for non-reproductive females (Figure 3.5), such that the logistic regression predicted non-reproductive females would have a greater probability of overwinter survival than those which weaned litters at densities greater than 17 per ha. However, the survival of females that weaned litters at densities greater than 17 per ha is an extrapolation of the data from smaller populations since there were no females in the population of 30.1 per ha that weaned a litter. Therefore that combination was not included in the model fitting, and as a result, caution must be taken when considering the predictive ability of the logistic regression equations at high densities for that category.

The high overwinter survivorship of females that weaned litters (71%, N = 14) combined with their low index of condition (Table 3.8) may have generated the peculiar negative relationship between condition and survival. However, when fall condition of all survivors was compared with non-survivors, average indices were nearly identical (Table 3.9). Condition may be insufficient to accurately predict overwinter survival. For example, manipulations supplementing food and/or excluding predators from ground squirrel populations had significant influences on mass and condition but failed to generate any differences in their overwinter survival rates (Hubbs and Boonstra 1997; Karels et al. 2000; Chapter 2). Factors other than the accumulation of body mass must play a major role in the overwinter survival of arctic ground squirrels.

It is unlikely that the low overwinter survival of females that had failed during lactation is related to a difference in their hibernating environment compared with the hibernating environment of females who were non-reproductive or weaned their litter. Differences in energy expenditure among hibernating individuals may be influenced by the thermal environment of their hibernaculum owing to ambient above ground air temperatures, physical soil properties, hibernacula depth (Young 1990), snow cover (King et al. 1991; Bryant 1998), sociality (Arnold 1990; Arnold 1995; Blumstein and Arnold 1998), nesting material (Young 1988), or composition of diet prior to hibernation (Frank 1992; Thorp et al. 1994; Frank and Storey 1995; Florant 1998). Food caching before hibernation may also influence overwinter survival but only male ground squirrels cache food (McLean and Towns 1981; Michener 1993). Ground squirrels are solitary hibernators and thus do not socially thermoregulate during hibernation (Arnold 1993). Hibernacula nesting material, which is composed primarily of grasses (Mayer 1953; personal observation), was abundant on all my study sites, especially on high-density sites where overwinter mortality was the greatest. Ambient above ground air temperatures were most likely similar among hibernating squirrels because study sites were within 150-m elevation and 20-km distance of one another. However, locations where individual squirrels hibernate may differ in snowpack, hibernacula depth, and soil characteristics depending on age (juvenile or adult) and sex of the squirrel (Shaw 1926; Buck and Barnes 1999b). However, this does not explain the differences in survival among the different reproductive classes of females in my study since all squirrels were adult females. I have no evidence to suggest that females with different reproductive histories would select different quality hibernacula.

Diet induced changes in hibernation patterns, metabolic rates, and body temperature have been demonstrated in several species of hibernating rodents. Studies that have increased the essential fatty acid content of food for hibernating rodents show decreased total energy expenditure during hibernation through increased duration of torpor bouts, reduced metabolic rates, and lowered minimum body temperature (Geiser and Kenagy 1987; Geiser 1991; Frank 1992; Florant et al. 1993; Geiser and Kenagy 1993; Thorp et al. 1994), all of which increase survival (Frank 1992). Furthermore, experiments have shown that diet selection by golden-mantled ground squirrels *S. lateralis* is based on fatty acid content (Frank 1994; Frank et al. 1998). Increasing concentrations of essential fatty acids in fat depots later in the season just prior to hibernation have been shown for free ranging rodents (Frank 1994; Hill and Florant 1999), including Siberian arctic ground squirrels (Sheikina and Serdiuk 1978). Thus, it seems likely that the role of essential fatty acids in hibernation also applies to the arctic ground squirrel but this hypothesis remains to be investigated.

Intraspecific competition for essential fatty acids may be the underlying mechanism that generated the negative relationship of population density and overwinter survival in natural populations. Because fat quantity alone appears to be unimportant in ensuring overwinter survival, fat quality seems a plausible explanation to explain how survival could be negatively associated with body condition. However, competition for fatty acids as an explanation for the differences in survival among reproductive classes, implies that there is differential access to resources among individuals within populations. Differential access to resources among females in a population may result from social dominance, differences in home range habitat, distance to closest neighbour (e.g. related individuals sharing a burrow system), or local interspecific competition (e.g. snowshoe hares *Lepus americanus*). I did not measure these fine scale individual differences and thus cannot test these hypotheses. This remains an important area for future studies in the role of microhabitat differences in population dynamics of arctic ground squirrels.

Positive and negative associations of life history traits

Arctic ground squirrels showed positive associations of life history traits similar to those shown in Columbian ground squirrels that Dobson et al. (1999) believed were indicative of 'increasing returns' where small initial investments are rapidly compounded. Female arctic ground squirrels in good spring condition were more likely to give birth, wean their litter, survive to the next breeding season, and breed again. It is still unknown if the explanation is simply that these females simply had more access to resources than the rest. Positive phenotypic correlations may be generated by differences among individuals where those that have greater access to resources are able to allocate more energy to offspring and survival relative to others living in poorer habitats; thus these correlations are not evidence against costs of reproduction (Reznick 1985).

In my study, as population density increased, the probability of overwinter survival of females that weaned litters declined at a greater rate than that of non-reproductive females, suggesting a cost of reproduction. Costs of reproduction have been used to explain senescence in animals where fecundity and survival decrease with age after first reproduction (Williams 1957; Stearns 1992) such as in this study where squirrel survival during the summer declined by a factor of 2.3 and survival during the winter declined by a factor of 7 for every year beyond the first year of reproduction. Since most of the non-reproductive females that survived for a year, attempted to breed the following season, it appears that not breeding or aborting their litter prior to lactation could be a strategy to increase long-term reproductive fitness. On the highest density site, the percentage of females that were non-reproductive was 2 - 4 times that on lower density sites (Figure 3.6). Neuhaus' et al. (1999) conducted a study of Columbian ground squirrels over three years with consecutively poorer environmental conditions. In their study, they showed that during the best and worst years, similar proportions of females in the population failed during lactation (15 and 16%), however, over the same period the proportion of non-reproductive females (females that did not give birth) increased from 8.3% to 65.7%. However, there was no evidence indicating an individual strategic effort to survive to the next breeding period. It may be that the population was simply below a resource per capita threshold necessary for females to allocate enough energy to a full term of gestation.

Expression of phenotypic costs at high densities was also discovered in a long-term study of bighorn ewes (*Ovis canadensis*). Festa-Bianchet et al. (1998) found reproduction was affected by an interaction between population density and ewe mass, where heavier ewes were more successful and experienced lower somatic and fitness costs than lighter ewes but only at high densities when food resources were limiting. For ground squirrels, costs of reproduction have been described for female European ground squirrels (*S. citellus*) (Huber et al. 1999), male arctic ground squirrels (Boonstra and McColl 2000) and in female Columbian ground squirrels (Festa-Bianchet and King 1991), yet, other studies on Columbian ground squirrels have not detected such costs (Murie and Dobson 1987; Hare and Murie 1992; Risch et al. 1995). However, Dobson et al. (1999) admit that to fully understand the evolution of life histories, an understanding of both positive and negative associations in life history traits is required.

Differential access to food resources may be the underlying factor determining the life history patterns of ground squirrels. However, increasing returns or reproductive costs do not fully explain the phenomenon where females who fail during lactation are the least likely to survive. Their spring condition is better but survival is poorer than that of non-reproductive females. Reproduction does not appear to be the cause of their mortality as they are in similar condition at the time of juvenile weaning and prior to hibernation as compared with females who are non-reproductive. In presenting possible explanations for the variation in different weaning success, survival to fall, and overwinter survival, there was common underlying factor, which provides one possible explanation. The actual explanation may lie within the quality of food. Essential fatty acids (linoleic, α linolenic) are important for proper lactation, milk quality, offspring growth and development (Jenkins and Kramer 1985; Henry et al. 1996; Francois et al. 1998; Chouinard et al. 1999; Sanders 1999) and are indispensable for hibernation in hibernating rodents (Florant 1998). Pond (1998) claims that in some environments the rarity and requirement for essential fatty acids may be a very important factor, more so than protein or carbohydrates, that determines the habits and habitats of animals. There is a need for studies to determine whether or not essential fatty acids are limiting reproduction and survival in natural ecosystems. They may prove to be an important factor determining the life-history strategies of hibernating rodents.

Chapter 4

HIBERNACULA SELECTION BY ARCTIC GROUND SQUIRRELS: THE IMPACT OF VEGETATION AND SNOW ON SOIL TEMPERATURES, MASS LOSS, AND SURVIVAL

Introduction

Animals that undergo long periods of winter hibernation have only one opportunity to select the location that will ensure their survival to spring. For hibernating fossorial rodents such as ground squirrels (*Spermophilus sp.*) this means constructing an underground hibernaculum that offers protection from predators and weather, and that minimizes their energy expenditure. Accumulated fat reserves are necessary for survival during hibernation (Michener 1974; Slade and Balph 1974; Murie and Boag 1984) but the rate at which fat reserves are consumed depends on a number of other factors. First, the composition of fat reserves (Florant 1998) and the presence and size of caches (Michener 1993) can alter the net loss of fat reserves overwinter. Second, factors that influence the thermal environment of the hibernaculum (Chappel 1981; Anufriev and Akhremenko 1990; Arnold et al. 1991; Arnold 1993) have direct impacts on energy expenditure during hibernation. Ground squirrels can minimize their exposure to extreme low temperatures by adjusting the quality and quantity of insulation in their hibernacula (Young 1988) or by varying the depth at which the hibernacula is constructed (Young 1990; Buck and Barnes 1999b). However, on the ground surface, snow depth positively influences soil temperatures by acting as a layer of insulation (Buck and Barnes 1999b).

Some habitats accumulate more snow (Young 1990; Buck and Barnes 1999b) and hence are warmer than others (Buck and Barnes 1999b). If there are fitness benefits for ground squirrels hibernating under these warmer habitats then natural selection should have favoured those squirrels choosing hibernacula in habitats that are likely to accumulate the most snow.

Arctic ground squirrels (*Spermophilus parryii*) are found throughout the mainland arctic tundra and the northern boreal forests of Canada and Alaska (Howell 1938) and spend approximately 7-8 months in winter hibernation (McLean and Towns 1981; Buck and Barnes 1999a). Minimum soil temperatures where squirrels hibernate in the boreal forest are unknown but in the arctic, minimum soil temperatures surrounding hibernacula can range from -8.9°C (Mayer 1955) to -23.4°C (Buck and Barnes 1999b). Although, arctic ground squirrels can maintain core body temperatures as low as -2.9°C, they begin to thermoregulate at temperatures < 0°C, the lowest head and neck temperature they can sustain (Barnes 1989). Anufriev and Akhremenko (1990) measured average energy expenditure of arctic ground squirrels during hibernation and found that energy expenditure of ground squirrels kept at -5°C was 1.7 times that of ground squirrels kept at 0°C (93.6 kJ/day vs. 55.7 kJ/day respectively). The total difference in energy consumption was entirely attributed to changes in energy consumption within torpor periods where energy consumption differed 15-fold between squirrels kept at -5°C (48.2 kJ/day) and squirrels kept at 0°C (3.1 kJ/day). Based on their estimate of 35.9 kJ/g, squirrels hibernating at -5°C would lose 1.1g/day of mass. Such differences in the rate of mass loss could ultimately determine whether or not an individual survives the winter, or more subtly influence their ability to reproduce in the spring.

I tested the hypothesis that boreal forest arctic ground squirrels (*S. parryii plesius*) locate their hibernacula preferentially in habitat types that minimize their energy expenditure during hibernation. To test this hypothesis I had four major objectives during this study. First, I determined where ground squirrels hibernate and quantified the habitat to determine habitat preference. Second, I measured how snow depth varies among habitat types. Third, I measured how habitat influences soil temperatures during winter. Fourth, I determined how choice of hibernacula influences mass loss and survival.

Methods

Study area

This study was conducted along the Alaska Highway within the Shakwak Trench east of Kluane Lake in the southwestern Yukon Territory, Canada (61°N, 138°W; elev. 600 - 1000m). The Shakwak trench is a broad valley (3 – 8 km wide) described as a morainic plain (Rampton 1981) underlain with basal till, lacustrine deposits, dead-ice moraine, and alluvial deposits (Department of Public Works and U.S. Department of Transportation, Federal Highway Administration1977). Permafrost is rare and restricted to north facing slopes (Department of Public Works and U.S. Department of Transportation, Federal Highway Administration1977) as the area lies approximately 50 km south of the 'widespread discontinuous permafrost' region described by Brown (1967).

The area experiences a mean annual temperature of -3.9 ± 0.2 °C and receives an average of 284 ± 10 mm total annual precipitation (data from Burwash Landing Climatological Station 1967-1995). The climate is classified as cold continental and snow cover exists from October to early May (Boutin et al. 1995) with an average depth of 55 cm (Murray and Boutin 1991). There are four major vegetation types in this valley: white spruce forests (*Picea glauca*) cover 50% of the area and have an understory of willow (*Salix* spp.) and birch (*Betula glandulosa*); shrub meadows of willow and birch cover 33%; grass meadows cover 7% (Boutin et al. 1995); and trembling aspen (*Populus tremuloides*) stands (10%) are sparsely distributed among the three other vegetation types (C. J. Krebs pers. comm.).

Live trapping

Arctic ground squirrels were live trapped from 1993-1996. Trapping commenced in early April to early May and ended in late August in all years. Study sites were trapped on average every two weeks with the exception of intensive census trapping (3-4 consecutive days per site) conducted in early May, in late June at juvenile emergence, and in late July to early August prior to adult female immergence into hibernation. Squirrels were captured using Tomahawk live traps (14 × 14 × 40 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with peanut butter. Traps were permanently placed at burrow openings and set at 0700 and checked twice at 1-1.5-h intervals. Each squirrel was removed from the trap into a netted bag and marked in each ear with uniquely numbered metal eartags. At each capture I recorded eartag number, sex, weight, and zygomatic arch breadth.

Arctic ground squirrels (N = 88) were fitted with radio transmitters (Model # PD-2C, Holohil Systems, Carp, Ontario) each August (24 in 1993, 34 in 1994, 30 in 1995) on one 10 ha control and on three 8-10-ha experimental sites all marked in an x - y grid with wooden stakes spaced 30 m apart. The experimental sites are briefly described as follows in order of increasing ground squirrel density (details in Karels et al. 2000):

1. *Predator Exclosure.* A 1-km^2 area was enclosed within a 2.2-m high 8600 V electric to keep out large mammalian predators (lynx [*Lynx canadensis*] and coyotes [*Canis latrans*]). Within the fenced area and over the ground squirrel trapping area, a 9 ha area

was covered with a barrier of nylon monofilament (2 m above ground spaced 20 cm apart) to exclude avian predators.

2. *Food Addition.* From 1988 to March 1996 supplemental food (commercial rabbit chow; 16% protein; Shur-Gain, Maple Leaf Foods Inc. Edmonton, Alberta) was provided *ad libitum* over a 36-ha area.

3. *Predator Exclosure + Food.* The above two treatments were combined on a 1-km^2 area in 1988 using the same protocols described above. A monofilament barrier was not erected and thus this treatment was strictly a mammalian predator exclosure.

Summer burrow and hibernacula locations

Sleeping burrows used during the summer were located in order to determine if in winter, squirrels use the same burrows or construct different burrows for hibernation. The location of summer burrows for males and juveniles were identified by live-trapping where squirrels captured ≥ 3 times at one location at first daily capture from July to August were assigned that location as their summer burrow. Adult females were radio-collared and the location of summer burrows identified while the females were sleeping (Karels et al. 2000). The locations of hibernacula for every radio-collared squirrel were located once during one week in mid-February in 1994, 1995, 1996 via radio-telemetry. The position (x - y coordinate), snow depth (cm), and habitat structure (open, shrub, spruce) directly over hibernacula were recorded.

Habitat availability

To relate hibernacula locations to habitat at ground level, I assessed the ground area covered by shrubs, spruce trees, and open habitats in the summer of 1994. The following criteria were used to identify each habitat. For shrubs, only those taller than 50 cm with multiple branches covering an area of at least 0.25 m^2 were used. Multiple shrubs that had branches that overlapped one another were measured as a single shrub. For spruce trees, only those with the lowest branches greater than 50 cm above the ground were included. Open habitats included all those areas greater than 0.25 m^2 with bare ground or herb vegetation. Shrubs, deadfall, or spruce seedlings that were shorter than 50 cm were also included within open areas. For each habitat type, I considered the total available to ground squirrels as being the product of two parameters; the number (e.g. number of trees) and area covered by the habitat (e.g. mean ground area covered by a tree). The density of each habitat type was estimated using T-square sampling procedure described in Krebs (1999). For each site I randomly selected 30 x - y coordinates within the 8-10-ha squirrel-trapping area using a random number generator. To determine the density of spruce trees, I took two distance measurements: the distance (m) from the each random location to the main stem of the closest spruce tree and the distance from that tree to the stem of the closest neighbouring spruce tree that was within a 90° angle of the first point to tree line. Population density was estimated using the robust estimator of Byth (1982) implemented in program Ecological Methodology (Krebs 1998). I used the same protocol for shrubs and open areas with the exception that the center of the shrub (or open area) was considered the closest point. The location of the center of shrubs and open areas was estimated by laying out a measuring tape across the maximum diameter and locating the halfway point then laying another measuring tape perpendicular to the first tape on that point. The point on the second tape that represented the half-way distance across the habitat type in that orientation was considered the center.

The relative contribution of each habitat type to area of ground covered independently of density was calculated from the average area covered by each (N = 60). During T-square sampling, I measured the radius of each spruce tree (center of stem to outer most branches) and calculated the area as a circle. For open habitat and shrubs, I measured the longest diameter and the perpendicular diameter to that and calculated the area as an ellipse.

The relative availability of habitat for each site was determined by multiplying the relative average area for each habitat type with the relative density of each habitat type.

Snow depth

I determined the average snow depth during mid-February on each site for each of the three winters by measuring snow depth with a 1 m metal ruler at a total of 30 stations at 30 m intervals along three parallel 300-m transects that were separated by 120 m.

I used the same transects described above to determine the influence of habitat on snow accumulation. At each station, I measured snow depth at the center of the closest shrub, the center of the closest clearing, and under the closest spruce tree at half the distance from trunk to edge of branches. Habitat types were identified with the same criteria previously described for habitat availability measurements. Snow measurements were taken during February 1994 only, but were measured at four additional sites over a 30-km section of the Alaska highway for a total of 240 stations.

Soil temperatures

To determine the influence of above ground habitat on soil temperatures during winter, I measured soil temperatures under shrubs, open areas, and spruce trees (half the distance between stem and outer branches) at a depth of 1 m. Eighteen temperature data loggers (Hobo-Temp, Onset Computer Corporation, Pocasset, MA) were set to record temperature every 3.2 hours from 7 September 1996 to 3 May 1997, and sealed in plastic to be buried below ground. To minimize the effect of possible confounding factors such as slope of the terrain, soil type, and geographic location, all data loggers were located along a 150 m transect on one of the study areas (Food Addition). The closest shrub, open area, and spruce tree at every 30m interval along the transect were selected (i.e. N = 6 for each habitat type). The organic layer, including above ground vegetation, was removed intact (30-cm diameter) at each location and a 30-cm diameter hole dug to a depth of 1 m. Before the data logger was placed in the hole, it was fastened to a stainless steel wire that was attached at the other end to a 30-cm wooden stake located 50 cm from the hole. Wire was used instead of more fragile materials to anchor the data logger for three reasons. It served as an aid to retrieve the data logger, it was resistant to damage while excavating the hole during the spring, and it was resistant to damage by animals. Temperature conductance along the wire was assumed to be minimal. The hole was filled in with the same soil and the organic layer was replaced intact and level with the surrounding terrain. Two additional temperature data loggers were set to record temperature at the same intervals as for the below ground data loggers but were positioned to measure ambient air temperatures. These two data loggers were sealed in a 11 × 7.5-cm diameter metal can to prevent damage by animals, sealed in plastic to keep out moisture, wrapped in white fiberglass tape to reflect solar radiation, and suspended 2 m above ground at each end of the transect.

For each data logger I calculated the number of accumulated degree hours below three reference temperatures: 0°C—the lowest neck and head temperatures of hibernating arctic ground squirrels (Barnes 1989); -2.9°C—the lowest core body temperature of a hibernating arctic ground squirrel (Barnes 1989); and -5.1°C—the soil temperature at 1 m soil depth where Barnes and Ritter (1993) found arctic ground squirrels reached their minimum core body temperature. Degree hours were calculated as the total accumulated departure of degree hours less than the reference temperatures where temperatures above the reference temperature were considered as zero (Boyd 1979).

Statistical Analysis

All statistical tests were performed according to procedures in Zar (1984) and Sokal and Rohlf (1995). Prior to all parametric statistics, all continuous variables were tested for the assumptions of parametric statistics using an *F*-test for equality of variances, and Kolmogorov-Smirnov goodness of fit test for normality. Data for calculating the mean snow depth per site per year and for snow over hibernacula were log-transformed and estimated means and 95% confidence limits were calculated using equations provided by Sokal and Rohlf (1995). All proportion data were arcsine transformed prior to parametric tests. Linear regression analyses were performed using program StatView (SAS Institute Inc. 1998), log-linear analyses were performed using program JMP-IN (SAS Institute Inc. 1997), and ANOVA and Tukey-Kramer post-hoc tests were performed using program SuperANOVA (Gagnon et al. 1991). All means are expressed with ± 1 S.E. unless otherwise indicated.

Results

Hibernacula habitat preference

The relative average area of an individual habitat patch (Table 4.1) and relative density (Table 4.2) of habitat patches were used to calculate the relative amount of habitat available (Table 4.3) to arctic ground squirrels when deciding where to locate their hibernacula. Individual spruce trees had a greater ground coverage than shrubs or open areas (Table 4.1) but because of the low numbers of spruce trees (Table 4.2) they ranked lowest in proportion habitat available (Table 4.3). The habitats were ranked as follows: open > shrub > spruce. The relative density of each habitat (Table 4.2) as estimated by T-square sampling differed among the sites ($\chi^2 = 450$, d.f. = 6, $P < 0.001$). Therefore, habitat preference was analyzed separately by site.

Of the 88 squirrels equipped with transmitters during late fall, 78 were located during the following mid-February, nine transmitters failed, and one squirrel was killed by a predator prior to immergence into hibernation. Arctic ground squirrels were not found to hibernate together as only one radio-collared squirrel was found per location. More than half (56%) of the squirrels hibernated under open areas, 28% under shrubs, and 8% under spruce trees. Manly's α index of habitat preference (Table 4.3) was calculated to determine whether ground squirrels located their hibernacula randomly relative to habitat. On three of the four sites, ground squirrels strongly avoided hibernating under spruce trees. Only on the predator exclosure site did ground squirrels show a preference for spruce (N = 3) while avoiding shrubs. There was no clear preference of open habitat over shrub habitat among the sites. Ground squirrels showed strong preferences for open areas on two of the sites (Manly's $\alpha > 0.40$) and strong preferences for shrubs on the other two sites (Manly's $\alpha > 0.45$).

Selection of hibernacula was not dependent on the location of prior summer burrows since only 4% (N = 70) of ground squirrels hibernated within 5 m of their summer burrow system. The distance between the summer burrow and the hibernaculum averaged 24 m (range 0 m - 111 m) but differed among the treatments with distance being significantly less on the predator exclosure + food site (Table 4.4 and Table 4.5). The average distance from summer burrow to winter hibernacula for each site and year declined significantly with increasing population density ($r^2 = 0.53$, d.f. = 9, $P = 0.01$) (Figure 4.1).

Table 4.1 Average area of an individual habitat patch (m^2) and relative area of ground coverage by an individual habitat patch (open areas, shrubs, and spruce trees, N = 60 per site) on four sites in the boreal forest of Kluane, Yukon. For spruce, an individual tree represents a patch.

Site	Open		Shrub		Spruce	
	m^2	Rel.	m^2	Rel.	m^2	Rel.
Control	2.53 ± 0.27	0.23	1.08 ± 0.17	0.10	7.24 ± 0.77	0.67
Predator Exclosure	3.05 ± 0.45	0.35	0.92 ± 0.18	0.11	7.72 ± 0.45	0.54
Food Addition	4.52 ± 0.92	0.40	1.38 ± 0.21	0.12	5.28 ± 0.66	0.47
Predator Exclosure + Food	6.18 ± 0.95	0.37	1.50 ± 0.21	0.09	9.17 ± 1.05	0.54

Table 4.2 Density (number per ha), 95% confidence limits and relative density of three habitat types (open areas, shrubs, spruce trees; N = 30 random points per site) estimated from T-square sampling on four study sites within the boreal forest of Kluane, Yukon.

Site	Open			Shrub			Spruce		
	No. per ha	95% C.I	Rel.	No. per ha	95%C.I.	Rel.	No. per ha	95% C.I.	Rel.
Control	865	603 - 1532	0.25	2310	1751 - 3396	0,67	270	185 - 501	0,08
Predator Exclosure	1278	948 - 1964	0.28	3078	2416 - 4241	0,67	227	153 - 438	0,05
Food Addition	1165	891 - 1682	0.38	1532	1116 - 2441	0,50	354	247 - 622	0,12
Predator Exclosure + Food	801	619 - 1134	0.37	1072	854 - 1441	0,50	294	229 - 408	0,14

Table 4.3 Manly's α index of arctic ground squirrel preference of habitat type for location of hibernacula in the boreal forest of Kluane, Yukon. Proportion of habitat available was calculated from the relative area of ground coverage (Table 4.1) and relative density (number per ha) (Table 4.2) of each habitat type. Ground squirrels were fitted with transmitters in fall prior to hibernation and located by radio-telemetry during mid February. Manly's α > .33 = preference, Manly's α < .33 = avoidance

Site	**Habitat**	**Proportion available**	**Number of hibernacula**	**Manly's α**
Control	Open	.33	9	.72
	Shrub	.38	4	.28
	Spruce	.29	0	0
Predator Exclosure	Open	.50	11	.40
	Shrub	.36	4	.20
	Spruce	.14	3	.40
Food Addition	Open	.57	16	.36
	Shrub	.23	8	.45
	Spruce	.20	3	.19
Predator Exclosure	Open	.53	8	.19
+ Food	Shrub	.17	12	.81
	Spruce	.29	0	0

Table 4.4 Four-way ANOVA of distance from summer burrow to hibernacula of arctic ground squirrels (N = 73) in the boreal forest of Kluane, Yukon.

Effect	d.f.	*F*	*P*
Year	2	1.0	0.38
Treatment	3	6.2	0.001
Sex	1	2.5	0.12
Age	1	0.2	0.63
Year × Treatment	5	0.8	0.58
Year × Sex	2	2.0	0.14
Year × Age	2	0.1	0.89
Treatment× Sex	3	2.1	0.12
Age × Treatment	3	0.2	0.89
Age × Sex	1	0.8	0.38

Table 4.5 Mean and 95% confidence limits of distance between summer burrow and winter hibernacula of arctic ground squirrels on four sites within the boreal forests of Kluane, Yukon.

Site	N	Distance (m)*	95% Confidence Limits
Control	12	31.7^{a}	19.1 - 52.6
Predator Exclosure	17	39.3^{a}	28.4 - 54.2
+ Food	23	23.7^{ab}	16.0 - 35.1
Predator Exclosure + Food	18	11.9^{b}	7.6 - 18.8
All Sites	70	23.6	18.9 - 29.5

*Identical superscripts indicate no significant difference (Tukey Kramer post-hoc).

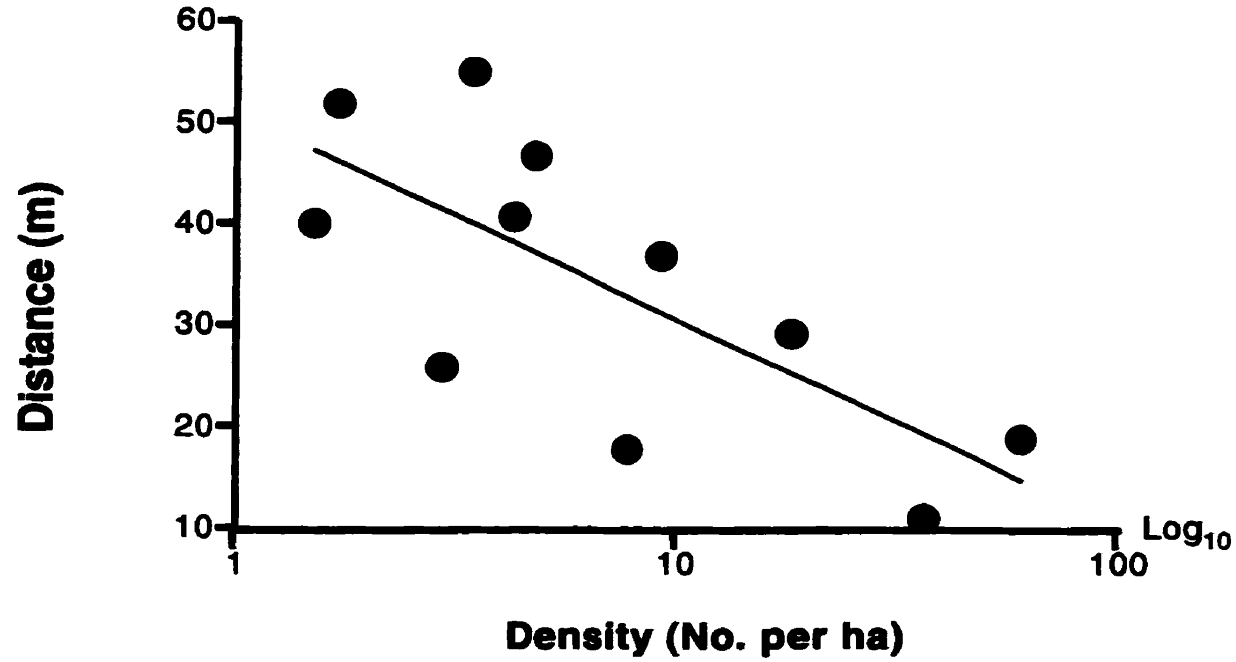


Figure 4.1 Regression of average distance (m) from summer burrow to winter hibernacula of arctic ground squirrels on four sites from 1994 to 1996. Nonlinear regression equation is y = -20.3 Log (x) + 51.0, $r^2 = 0.53$, $P = 0.01$.

Snow depth

The average snow depth over hibernacula was neither significantly nor consistently greater than that over systematic sampling locations (Figure 4.2, Table 4.6). Only on the control site in 1995 and the predator exclosure + food site in 1996 was snow depth over hibernacula significantly greater than each site's average snow depth. Average hibernacula snow depth was never significantly less than the site average (Table 4.6). Average snow depth tended to differ among the four sites (two-way ANOVA: $F_{3,347} = 2.6$, $P = 0.05$) and differed significantly among years (two-way ANOVA: $F_{2,347} = 50.0$, $P < 0.001$) but in an interactive manner (two-way ANOVA site × year: $F_{6,347} = 3.4$, $P = 0.003$). Similarly, the snow depth over hibernacula differed significantly among years and sites (Table 4.7). Furthermore, it differed significantly among habitat types (Table 4.7), where there was significantly less snow over hibernacula under spruce trees (27 ± 4.6 cm, N = 6) than over hibernacula under shrubs (58 ± 2.9 cm, N = 28) or under open clearings (54 ± 2.2 cm, N = 44) (Tukey-Kramer post-hoc, $P < 0.05$). Snow depth over hibernacula under shrubs did not differ from that under open clearings (Tukey-Kramer post-hoc, $P > 0.05$). Snow depth in the Kluane area differed significantly by site but interactively with habitat type (Table 4.8). At systematic sampling locations at eight sites, habitats were ranked by decreasing snow depth as follows: opening ≈ shrubs > spruce (Figure 4.3). However, because of the greater sample size, I detected a small (6%) but significant difference between snow depth in shrubs and open clearings where the latter had 3 cm less snow cover (Tukey-Kramer post-hoc, $P < 0.05$). Snow depth under spruce trees was approximately 60% less than that under shrubs and open clearings

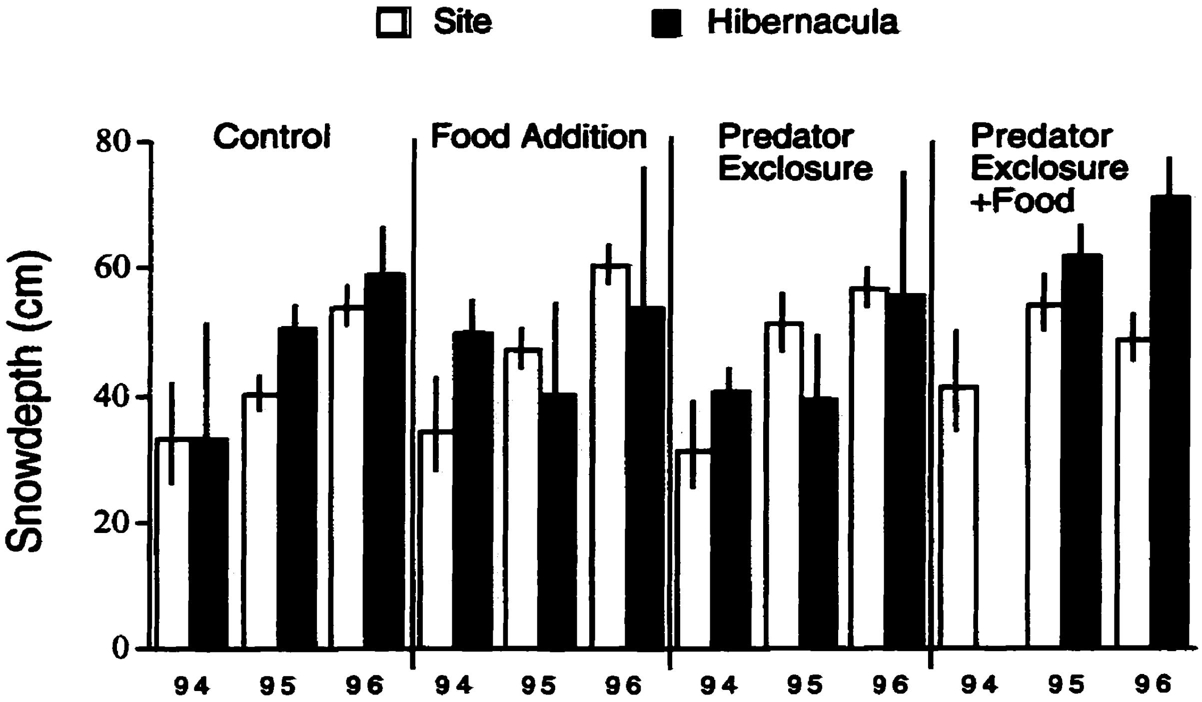


Figure 4.2 Estimated mean snow depths (cm) with 95% confidence limits of each site in systematic locations (N = 30 per site per year) and over the hibernacula of squirrels (see Table 4.3 for squirrel sample sizes).

Table 4.6 Mann-Whitney U-test pairwise analysis of snow depth over arctic ground squirrel hibernacula and snow depth over systematic sampling locations among treatments and years. Squirrels were radio-collared in fall prior to hibernation in three years on four different sites at Kluane, Yukon.

Grid	Year	Hibernacula (N)	Site (N)	*Z*	*P*
Control	1994	3	30	0.12	0.9
	1995	6	30	3.00	0.003*
	1996	4	30	0.96	0.34
Predator Exclosure	1994	5	30	1.56	0.12
	1995	7	30	0.14	0.89
	1996	6	30	0.57	0.57
+ Food	1994	8	30	2.56	0.01
	1995	7	30	0.35	0.73
	1996	10	30	0.58	0.56
Predator Exclosure + Food	1994	0	30	-	-
	1995	11	30	1.72	0.085
	1996	9	30	3.68	0.0002*

*snow depth greater over hibernacula than over systematic sampling sites at significance level $\alpha = 0.004$

Table 4.7 Three-way ANOVA of mid-February snow depth over arctic ground squirrel hibernacula (N = 78) among four treatments, three years 94 - 96, and three habitats (open, shrub, spruce) in the boreal forest of Kluane, Yukon.

Effect	**d.f.**	***F***	***P***
Year	2	20.5	< 0.001
Treatment	3	4.4	0.007
Habitat	2	20.4	< 0.001
Year × Treatment	5	1.5	0.21
Year × Habitat	3	2.6	0.15
Treatment × Habitat	4	0.63	0.64
Year × Treatment × Habitat	4	0.50	0.74

Table 4.8 Two-factor ANOVA of snow depth measurements (N = 698) taken during mid-February 1994 in three habitat types (open, shrub, spruce) among eight sites located along a 30 km section of the Alaska Highway in the boreal forest of Kluane, Yukon.

Effect	d.f.	*F*	*P*
Site	7	65.5	<0.001
Habitat	2	1024	< 0.001
Site × Habitat	14	2.5	0.002

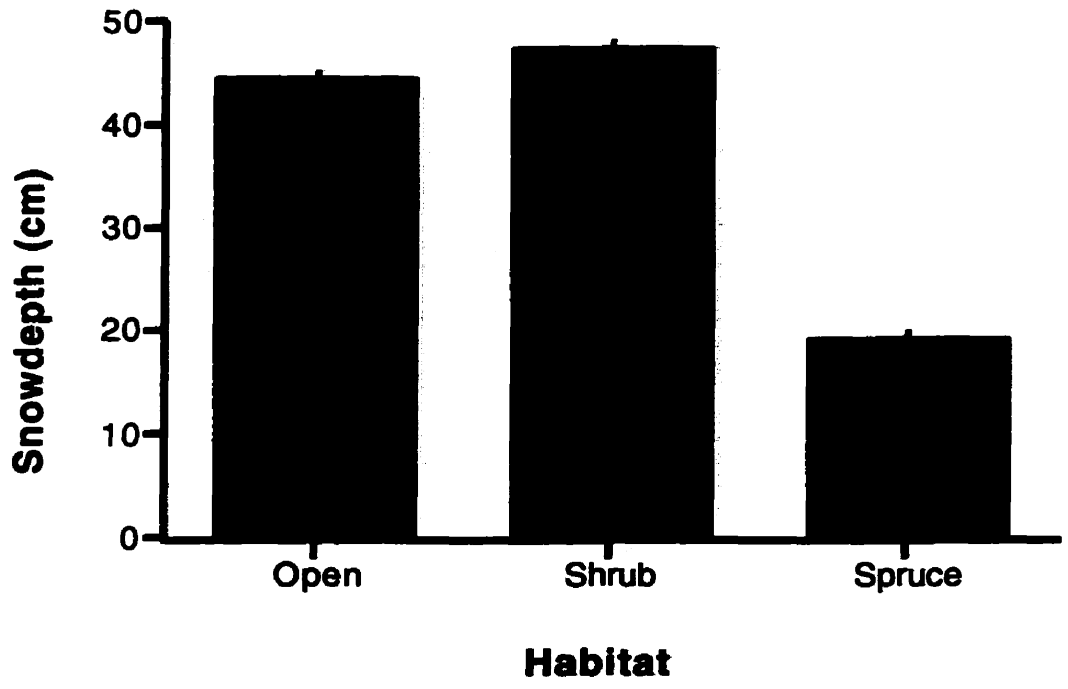


Figure 4.3 Mean snow depth taken from 698 measurements in three habitat types during mid-February, 1994. Samples were divided among eight sites located along a 30 km section of the Alaska Highway in the boreal forest of Kluane, Yukon.

(Figure 4.3). Snow depth over hibernacula was similar among male and female squirrels (two-way ANOVA: $F_{1,72} = 0.04$, $P = 0.84$) and among adults and juveniles (two-way ANOVA: $F_{1,72} = 2.1$, $P = 0.16$) and did not differ interactively (two-way ANOVA sex × age: $F_{1,72} = 0.12$, $P = 0.73$).

Soil temperatures

Two temperature data loggers at one sampling station failed during winter and thus only the temperatures from the other five stations (i.e. N = 5 per habitat type) are presented. Mean ambient air temperature and mean soil temperatures under open areas, shrubs, and spruce trees are shown in Figure 4.4. The number of degree hours less than -2.9°C differed significantly among the three habitat types habitat types (Kruskal-Wallace, d.f. = 2, $H = 6.3$, $P = 0.04$) with soil temperatures under spruce accumulating approximately 100 degree hours more than soil temperatures under shrubs or open clearings (Table 4.9). There were no temperatures recorded below -5.1°C underneath shrubs and open clearings. Soil temperatures under spruce trees accumulated 15.7 degree hours below -5.1°C. Minimum soil temperatures also differed significantly among habitat types (Kruskal-Wallace, d. f. = 2, $H = 7.1$, $P = 0.03$) with minimum temperatures under spruce trees being 2.5°C less than the minimum temperatures under shrubs and open areas.

Survival and mass changes

Because only male ground squirrels cache food prior to hibernation (McLean and Towns 1981), I excluded them from the following analyses of mass loss and survival over winter. Over the course of the study, five adult females and six juvenile females died overwinter. Survival was independent of age, site, snow depth, and habitat (Table 4.10). Survival differed significantly among years (Table 4.10), with the most mortality occurring over the winter of 1995/1996 (50% of radio-collared squirrels, N = 16). The small number of mortalities prevented testing for interactions among factors influencing survival.

The amount of mass lost by female ground squirrels was positively related to fall pre-hibernation mass (linear regression: $r^2 = 0.26$, d.f. = 34, $P = 0.002$) whereas the proportion of mass lost was not (linear regression: $r^2 = 0.03$, d.f. = 34, $P = 0.34$). Therefore proportion mass lost should be a better index of energy expenditure. However, I performed analyses of both absolute mass loss and proportion of mass lost so that comparisons could be made with other studies. Absolute and proportion of mass lost over winter were similar among the sites (one-way ANOVA: absolute $F_{3,31} = 1.54$, $P = 0.26$; proportion $F_{3,31} = 1.14$, $P = .35$). Females were 154 ± 11g lighter in spring than before fall immergence corresponding to a 27% (95% C.L = 3 - 60%;) loss of mass over winter. Absolute and proportion mass lost differed interactively among age and year (two-way ANOVA age × year: absolute $F_{2,29} = 6.47$, $P = 0.005$; proportion $F_{2,29} = 5.05$, $P = 0.01$).

When over winter mass loss was analysed separately for each age class and year, absolute and proportion of mass lost declined non-significantly as accumulated snow depth over the hibernacula increased for all years and age classes except for 1996 (Table 4.11). In that year, mass lost increased non-significantly as snow depth increased for three juveniles (Table 4.11). When age classes were pooled, the relationship between mass lost and snow depth was stronger (Table 4.11). In 1994 and 1995, the proportion of

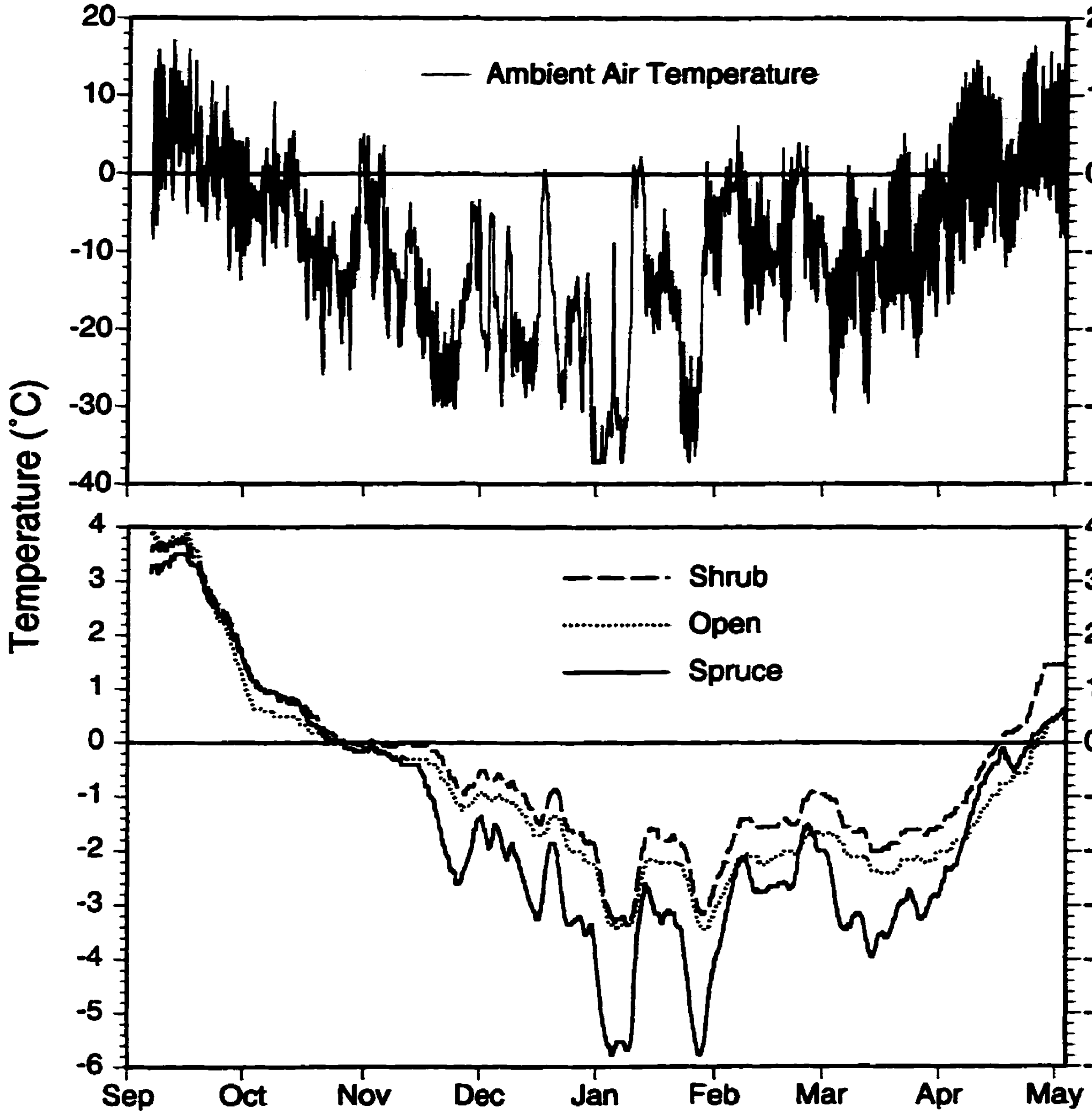


Figure 4.4 Mean ambient temperature (upper graph, N = 2 locations) and mean soil temperature at 1 m depth under shrubs, open clearings, and spruce trees (lower graph, all N = 5 per habitat type) from September 7, 1995 to May 3, 1996 in the boreal forest of Kluane, Yukon. Ambient temperatures < -37°C are not shown as this was below the minimum temperature recordable by the data loggers.

mass lost over winter declined as snow depth increased. However, in 1996, the proportion of mass lost tended to increase as snow depth increased owing to two juvenile females who lost little mass while hibernating under low snow depth (Figure 4.5). When these two individuals were excluded from the analysis the relationship was barely negative (slope of -0.01 per 10-cm snow depth, $r^2 = 0.03$, $N = 6$, $P = 0.74$), but there is no sufficient explanation to justify them as outliers and thus they are included in the analysis in Table 4.11 and Figure 4.5.

Table 4.9 Mean and minimum ambient air temperatures and soil temperatures at 1 m depth in three habitats shown as accumulated degree hours less than reference temperatures. Reference temperatures were: 0°C — the lowest head and neck temperatures of hibernating arctic ground squirrels (Barnes 1989); -2.9°C — the lowest core body temperature of a hibernating arctic ground squirrel (Barnes 1989); and < -5.1°C — the temperature at 1 m soil depth where Barnes and Ritter (1993) found that hibernating arctic ground squirrels reached their minimum core body temperature.

	Degree hours < 0°C		Degree hours < -2.9°C		Degree hours < -5.1°C		Minimum Temperature	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Ambient	2496 ± 128	2368-2625	1972 ± 117	1855 - 2089	1618 ± 105	1513 - 1723	-37*	-
Shrub	236.4 ± 61.0	93.4 - 452.6	11.4 ± 8.6	0 - 44.6	0 ± 0	0 - 0	-3.4 ± 0.5	-4.8 to -2.3
Open	309.4 ± 31.1	220.9 - 383.0	6.7 ± 2.3	1.3 - 11.8	0 ± 0	0 - 0	-3.5 ± 0.2	-3.8 to -3.1
Spruce	376.2 ± 82.8	96.3 - 590.0	107 ± 47.4	4.5 - 277.9	15.7 ± 11.1	0 - 59.3	-5.9 ± 0.8	-8.5 to -3.8

*minimum temperature recordable by data logger

Table 4.10 Log-linear analysis of overwinter survival of radio-collared female arctic ground squirrels at Kluane, Yukon, 1993 - 1996.

Effect	d.f.	Log-Likelihood	G^2	*P*
Age	49	26.58	0.02	0.90
Year	48	20.39	12.41	0.002
Site	47	26.02	0.77	0.78
Snow depth	50	25.02	2.79	0.09
Habitat	48	25.55	2.09	0.35

Table 4.11 Mean absolute (g ± S.E) and mean proportion (95% confidence limits) of mass lost over winter during hibernation for juvenile and adult female arctic ground squirrels **a)** separately, and **b)** ages pooled. Linear regression analyses was performed for both absolute and proportion mass loss with accumulated snow depth over hibernacula of female arctic ground squirrels in the boreal forest of Kluane, Yukon (1994 - 1996). The rate of mass lost is presented as the amount (or proportion) of mass change for every 10-cm increase in snow depth. Negative values represent decreasing mass loss with increasing snow depth and positive values represent increasing mass loss with increasing snow depth.

a) separate age classes

Age	Measure	Mean	Rate	N	r^2	*P*
		1994				
Adult	Absolute	262 ± 62	-156.2 ± -	2	-	-
	Proportion	0.41 (0.05 - 1.00)	-0.17 ± -	2	-	-
Juvenile	Absolute	92 ± 11	-4.6 ± 2.3	5	0.01	0.86
	Proportion	0.20 (0.13 - 0.26)	-0.02 ± 0.05	5	0.08	0.66
		1995				
Adult	Absolute	154 ± 20	-23.8 ± 10.1	11	0.34	0.06
	Proportion	0.25 (0.17 - 0.31)	-0.03 ± 0.02	11	0.26	0.11
Juvenile	Absolute	161 ± 12	-9.0 ± 10.4	9	0.10	0.42
	Proportion	0.32 (0.25 - 0.34)	-0.02 ± 0.02	9	0.14	0.32
		1996				
Adult	Absolute	193 ± 34	-2.1 ± 27.2	5	< 0.01	0.94
	Proportion	0.29 (0.18 - 0.36)	-0.01 ± 0.03	5	0.01	0.87
Juvenile	Absolute	95 ± 28	+20.5 ± 9.7	3	0.82	0.28
	Proportion	0.21 (0.01 - 0.51)	+0.05 ± 0.01	3	0.99	0.06

b) ages pooled

Year	Measure	Mean	Rate	N	r^2	*P*
1994	Absolute	141 ± 35	-85.0 ± 8.2	7	0.67	0.02
	Proportion	0.26 (0.15 - 0.34)	-0.09 ± .03	7	0.65	0.03
1995	Absolute	157 ± 12	-19.6 ± 7.6	20	0.26	0.02
	Proportion	0.28 (0.22 - 0.30)	-0.03 ± .01	20	0.20	0.05
1996	Absolute	156 ± 29	+ 19.4 ± 11.5	8	0.32	0.14
	Proportion	0.26 (0.17 - 0.32)	+0.02 ± .01	8	0.36	0.11

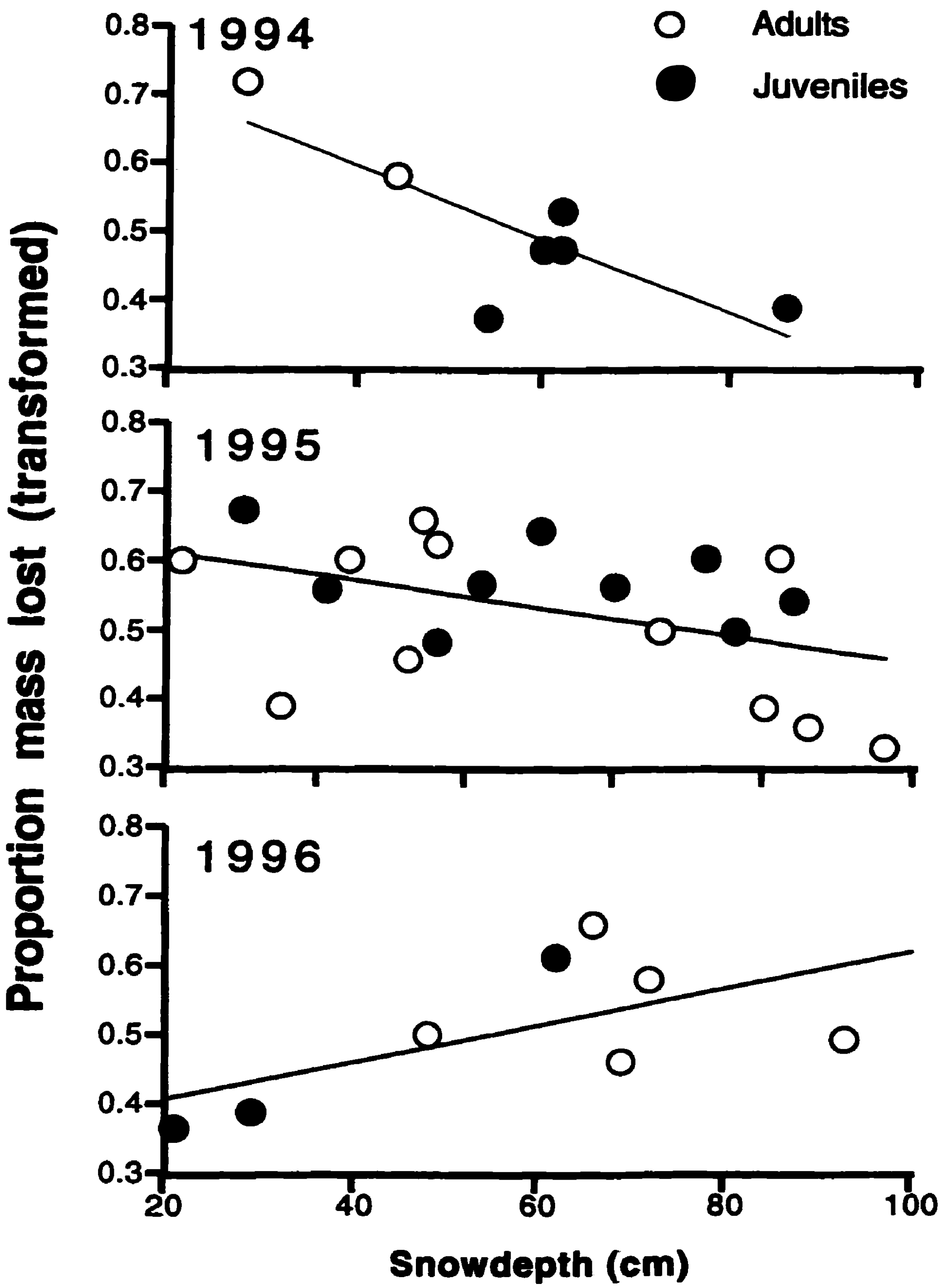


Figure 4.5 Proportion of mass lost (arcsine transformed) during hibernation by adult and juvenile female arctic ground squirrels from 1994 - 1996. Linear regression line shown for each year was calculated for both age classes pooled. Table 4.11 shows regression statistics for age classes separately and pooled.

Discussion

Arctic ground squirrels in the boreal forest located their hibernacula with respect to above ground habitat in a pattern that would minimize their overwinter energy expenditure. Ground squirrels hibernated under shrubs and open areas where snow accumulations were greater and soil temperatures were warmer and avoided hibernating under spruce trees where snow accumulations were 40% of that in the other habitats and soil temperatures were colder. In two of three winters, female ground squirrels tended to lose less mass with increasing snow depth over their hibernacula. Therefore by selecting habitats with the probability of accumulating the most snow, ground squirrels may increase their chances of overwinter survival and complete hibernation with greater residual fat stores for investment in reproduction.

Before discussing the results, there is one caveat that needs to be addressed. Over winter survival as measured by telemetry did not detect a direct cost of hibernating under poor conditions in survival and may be a poor indicator of overwinter survival. In fact, only three female squirrels (9% N = 35) were found to have died over the winters of 1993/94 and 1994/95 when trapping records indicated that overwinter survival averaged 56.7% and 73.2% respectively (Karels et al. 2000). Therefore radio-telemetry severely over estimated survival during these two years. During 1995/96, radio-telemetry estimated 50% (N = 16) of squirrels to have died overwinter which underestimated the average survival according to trapping records (67.6%) but was consistent with overwinter survival on the controls (51.6%) and on the predator exclosure (51.5%). Radio failure was greater in 1993/94 (21%) and 1994/95 (6%) than in 1995/96 (3%) and coincided with the degree of bias in the survival estimate. This suggests that squirrel survival and radio survival may be correlated possibly owing to the thermal influence of a living squirrel on the transmitter. A dead squirrel would mean colder operating temperatures for the radio transmitter and may increase the rate at which the battery is exhausted. Therefore I advise caution in the use of radio-transmitters for measuring over winter survival of hibernating animals in cold climates. Although the majority of my transmitters operated > 8 months, they were rated as 6-month longevity. Therefore I suggest that for these types of studies, transmitter longevity should exceed the duration of the hibernation period to reduce the possibility of animal and radio survival correlations.

Arctic ground squirrels in the boreal forest rarely located their hibernacula near their summer burrow (< 5%). Instead they located their hibernacula distantly from their summer burrows by approximately 24 m, which strongly suggests that different qualities of burrows are required for winter than for summer. Michener (1992) showed that Richardson's ground squirrels used their hibernacula only for hibernation. Excavators of Columbian ground squirrel (*Spermophilus columbianus*) hibernacula in Washington (Shaw 1926) and Alberta (Young 1990) distinguished the hibernaculum as a distinct chamber from the summer burrow system although they were sometimes connected. Hoary marmots (*Marmota caligata*) were found to have distinct hibernacula which they abandoned after snowmelt (Barash 1974; Holmes 1979). Svendsen (1976) estimated continued use of the hibernacula by yellow-bellied marmots (*Marmota flaviventris*) in Colorado during the summer as infrequent (< 8%) and suggested that subtle features of burrows make some more attractive than others in different situations. However, at higher elevations in Colorado, Andersen et al. (1976) found that most yellow-bellied marmots used their hibernaculum all year long. For arctic ground squirrels north of the

Arctic circle near Atkasook, Alaska, Batzli and Sobaski (1980) described burrows that served both as hibernacula in winter and as nurseries in summer. Buck and Barnes (1999b) also implied that hibernacula burrows are used throughout the year when they suggested that the location of hibernacula may be partially dependent on factors other than thermal quality such as food, visibility of surrounding terrain, and cover from predators. Suitable habitat for burrowing in arctic regions has been described as limited and restricted to eskers, lake and river banks, or any raised area where the permafrost table is relatively low (Mayer 1953; Carl 1971; Batzli and Sobaski 1980; Mallory and Heffernan 1987). Because of this limitation, arctic ground squirrels in arctic environments may be forced to hibernate in the same burrows where they also live during the summer.

Arctic ground squirrels in their southern range within the boreal forest appeared not to be limited by burrowing habitat in contrast to arctic ground squirrels in northern Alaska (Mayer 1953; Carl 1971). Carl (1971) claimed that the availability of hibernacula in that environment was the ultimate resource by which their populations were regulated. However, during my study when ground squirrels were given food and protected from predators, their populations reached densities nearly 6-fold (30.1 per ha) that found in Carl's (1971) study (5.5 per ha) without any reduction in overwinter survival when compared with controls (Karels et al. 2000). Therefore, hibernacula could not be limiting at lower densities in my study area. In contrast to the southern Yukon, the presence of permafrost and depth of thaw in northern Alaska are critical factors determining the depth and hence the thermal environment of hibernacula for arctic ground squirrels (Buck and Barnes 1999b).

Exclusion of predators, addition of food, or the combination of both treatments did not influence which habitat ground squirrels hibernate under (Table 4.7, Figure 4.2), their mass loss overwinter (Table 4.10), or their overwinter survival (Karels et al. 2000, this study). However, the distance from the summer burrow to the winter hibernacula was affected by treatment (Table 4.5) in such a manner that distance was negatively related to population density (Figure 4.1). High densities may force individuals to hibernate closer to home if there is increased aggression among individuals setting up hibernacula. Carl (1971) reported increased territoriality among both sexes and age classes of arctic ground squirrels in the fall on the north coast of Alaska. But near my study area, only males were reported to defend hibernacula (Lacey 1991), thus it is unclear if territoriality influences the distance that squirrels will go to construct hibernacula. The area in which a ground squirrel chooses a place to hibernate may be directly related to their home range during the summer. Hubbs and Boonstra (1998) found that the size of the home range of arctic ground squirrels on the same experimental treatments was negatively correlated with population density but suggested that differences in home range sizes were a result of treatment rather than density. Because nearly all activities except for hibernation are associated with the summer burrow it is unclear how food addition and predator exclusion influence the placement of the hibernaculum. A possible explanation is that the hibernaculum is constructed within the area that is most familiar to the squirrel—the summer home range.

Arctic ground squirrels in the boreal forest face seasonal changes in habitat suitability owing to conflicting pressures of predation and thermoregulation. Presence of predators and visibility through the habitat are important factors determining where arctic ground squirrels live in the boreal forest during their active season (Karels and Boonstra 1999) but not during the winter. I detected no effect of predator exclusion on location of hibernacula, which suggests that other factors such as those that influence the thermal environment of the hibernacula are more important. During the summer, arctic ground squirrels avoid constructing burrows in areas with poor visibility, such as shrubby habitats (Karels and Boonstra 1999). During the winter, shrubby habitats offer increased protection from cold ambient temperatures owing to likelihood of deeper insulating snow (Buck and Barnes 1999b, this study). When constructing hibernacula, ground squirrels avoid those habitats with the poorest possible thermal environments, such as under spruce trees where there is 57 - 59% less snow. But during the summer, predator detection near their burrows under the spruce canopy is high (Karels and Boonstra 1999) owing to exclusion of shrubs underneath the tree canopy.

North of the boreal forest and concurrent with my study, Buck and Barnes (1999b) measured winter soil temperatures at a maximum depth of thaw of 97 cm around arctic ground squirrel hibernacula. They found that hibernacula temperature differed among age and sex classes of squirrels and that burrows used exclusively by females (N = 7) were in shrubby areas where snow was deeper and burrows are warmer. However, they did not quantify the amount of habitat that was available for hibernation. Nevertheless their study does suggest that squirrels may have been able to discriminate among habitats for suitable hibernacula. Similarly, Young (1990) found sex and age specific hibernacula construction for Columbian ground squirrels and that at high elevations all Columbian ground squirrel hibernacula were found under shrubs or in shallow depressions which collected drifts. Preferences for locating hibernacula in habitats that are most likely to accumulate the most snow imply that there are costs when squirrels hibernate in suboptimal habitat.

Detection of costs of hibernating in poor habitats is difficult as few squirrels hibernate in poor environments. Furthermore, variation in energy expenditure of a hibernating squirrel owing to differences in quality and quantity of insulation in the nest (Young 1988), depth of the hibernacula (Buck and Barnes 1999b) or the quality of diet prior to hibernation (Florant 1998) may also confound detecting such costs. Buck and Barnes (1999b) found that minimum soil temperatures were considerably colder (-23.4 to -8.0°C) and female squirrels lost a greater proportion of their mass (35%) in northern Alaska than I found at my study site where minimum soil temperatures were warmer (-8.5 to -2.3°C) and female squirrels lost approximately 27% of their mass. But despite the colder conditions of the hibernacula in north Alaska, Buck and Barnes (1999b) did not find any relationship of absolute lean, fat, or total body mass loss with soil temperature. I did not measure soil temperatures around hibernacula but rather snow depth, which is correlated with soil temperatures owing to its insulative properties (Marchand 1991; Buck and Barnes 1999b). Snow depth over hibernacula did not differ among age classes. However, mass loss of hibernating females, whether calculated as absolute mass lost (Table 4.11) or proportion of fall mass lost (Table 4.11, Figure 4.5) increased as snow depth decreased in my study in two of three years. I did not detect any direct cost of reduced snow depth over the hibernacula to survival (Table 4.10), however, mass loss during the winter influences the condition of squirrels at spring. Squirrels in better condition are more likely to produce a litter (Chapter 3) and hence have greater fitness. Habitat dependent mass loss that influences survival and reproduction may be a mechanism that has selected for the ability of ground squirrels to identify habitats that minimize their energy expenditure during hibernation prior to winter conditions.

Chapter 5

CONCLUSION: POPULATION REGULATION, REPRODUCTION AND HIBERNATION IN ARCTIC GROUND SQUIRRELS

Summary

The objectives of my research were (1) to determine the mechanisms that regulate arctic ground squirrel populations in the boreal forest; (2) to determine how variation among individuals and their environment influences arctic ground squirrel reproduction and survival, and (3) to determine how variation in habitat influences hibernating strategies of arctic ground squirrels.

Arctic ground squirrels responded to population density with major changes in reproduction and survival such that populations, when experimentally perturbed from normal densities, converged in density to those of control populations within 2 years after removal of the Kluane Project's experimental manipulations. I will outline the main conclusions of my research, discuss briefly the role of density dependence in the 10-year cycle of arctic ground squirrels, and recommend further research to resolve unanswered questions.

Major findings:

(1) Arctic ground squirrel populations showed strong evidence of population regulation. Population densities on experimental sites declined at a density-dependent rate such

that densities on experimental sites approximated control population densities within two years after the experimental manipulations of food and predators terminated.

(2) Arctic ground squirrel populations showed strong density-dependent declines in weaning rate and in overwinter survival. Both of these operated through competition for food resources. For both parameters, the strength in density dependence remained similar from one year to the next. However, overwinter survival was the dominant mechanism reducing experimental populations back to control population densities.

(3) Density-dependent changes in weaning rate occurred simultaneously with density-independent changes in weaning rate. Whereas density-dependent changes in weaning rate were determined by intraspecific competition for food resources, density-independent changes in weaning rate appeared to be determined by winter snow depth acting through maternal condition.

(4) The probability of adult female squirrels giving birth increased with body condition but decreased with population density. Age of the female had no effect on birth rate. Weaning rate was strictly density-dependent and not influenced by condition or age.

(5) Survival during summer was inversely density dependent and decreased with age. However, females that lost their litters during lactation had a greater rate of mortality than females that never gave birth or that weaned their litter.

(6) Overwinter survival declined with increasing population density, increasing age, and increasing pre-hibernation body condition. For females that weaned a litter, mortality increased at a greater rate with population density in comparison with

females that never gave birth. However, nearly all females who lost their litter during lactation died overwinter.

(7) Arctic ground squirrels displayed a positive association among life-history traits such that females in better condition were more likely to give birth, wean their young, survive to the next breeding season, and reproduce once again.

(8) Herbivory increased with population density of ground squirrels and increased differentially among plant species. Legumes were highly preferred and were eliminated from sites with high squirrel densities when the food supplementation ceased.

(9) Arctic ground squirrels in the boreal forest select different burrow sites for hibernation than they do for their summer quarters. Their hibernacula occur in open areas and shrubby areas, both of which have greater snow cover and higher minimum soil temperatures.

(10) Overwinter mass loss of adult and juvenile squirrels decreased as snow depth over their hibernacula increased in two of three years. However, survival was unrelated to snow depth.

Discussion

Population dynamics of arctic ground squirrels in the boreal forest

Arctic ground squirrels in the boreal forest fluctuated 3-fold over the duration of the snowshoe hare cycle from 1990 to 1998 (Figure 5.1). Changes in population density were driven by density-dependent and density-independent factors that changed throughout the hare cycle. Figure 5.1 illustrates the dominant mechanisms of population change in four phases (❶ to ❹) of changes in arctic ground squirrel numbers during one complete snowshoe hare cycle.

❶ **Decline.** At Kluane, snowshoe hare numbers peaked in 1990 and declined from 1991 to 1993 (Boutin et al. 1995; Krebs et al. 1995). Ground squirrel numbers peaked one year later and declined sharply by 48 to 56% by 1992 (Hubbs and Boonstra 1997). Predation on ground squirrels was intense during this period (32 - 49% of radio-tracked individuals killed over a 3.5-month period) (Hubbs and Boonstra 1997) as both mammalian and avian predators were abundant and their main prey, snowshoe hares, were becoming scarce (Boutin et al. 1995). The experiments of the Kluane Boreal Forest Ecosystem Project demonstrated that both food and predators were limiting ground squirrel populations during this period (Hubbs and Boonstra 1997). Hubbs and Boonstra (1997) suggested that these two factors interacted to limit ground squirrel populations, but their evidence was not very strong as densities on the predators exclosure + food site surpassed those of the other treatments only in 1992, the last year of their 3-year study. It was not clear that predators were affecting ground squirrels in a density-dependent manner. My evidence (chapter 2) suggests that predators exert primarily density-independent influences on ground squirrel numbers. Therefore, I suggest that the decline phase in ground squirrels numbers was driven primarily by the effects of density-independent predation and possibly by density-independent sublethal effects of predators on squirrel reproduction.

❷ **Low.** By 1994, avian predators had declined by 50% and mammalian predators had declined by approximately 85% from peak numbers from 1990 -1992 (Boutin et al. 1995). Consequently, ground squirrel survival improved from 71% to 97% per 28-day period from 1993 to 1994 (Byrom et al. 2000). From 1993 to 1995 it was clear that ground squirrels were limited by an interaction between food and predators (Karels et al. 2000) and that direct predation had a declining influence on ground squirrel numbers (Byrom et al. 2000). However, although predators were less abundant at the low phase than during the decline phase, they still exerted sublethal effects on reproduction in ground squirrels. In the absence of predation, 16 to 37% more female ground squirrels weaned litters (Karels et al. 2000). Therefore, during the low phase in the hare cycle, ground squirrels are primarily limited by an interaction between food and predators operating through reproduction.

❸ **Increase.** From 1994, ground squirrel populations were essentially released from the limiting effects of direct predation as predator populations were low and snowshoe hare populations increased (Krebs et al. 1995). From 1994 to 1996, survival rates of ground squirrels were greater than 88% per 28 days [1994 = 88%, 1995 = 97% Byrom et al. (2000); 1996 = 97% (Chapter 2)]. However, predators still imposed sublethal effects that interacted with food availability to limit the maximum rate of reproduction (Karels et al. 2000). Thus during the increase phase of the hare cycle, ground squirrel populations responded to a new limit determined by both density-dependent reproduction (Chapters 2 and 3) and density-dependent overwinter survival (Chapters 2 and 3).

❶ **Peak.** Ground squirrels peaked in numbers in 1990-1991 and again in 1997-1998 after the near absence of predation after 1994. Density-dependent reproduction and density-dependent overwinter survival continued to determine the ground squirrel population density during the peak phase of the hare cycle (Chapters 2 and 3). However, reproduction was susceptible to density-independent fluctuations that appeared to be influenced by changing snowpack conditions (Chapter 2), which may have influenced energy expenditure overwinter determining the residual fat reserves in spring (Chapter 4). Survival during the active season declined from 97% in 1996 to 91% per 28 days in 1997 (Chapter 2), perhaps owing to increases in predator populations (C. J. Krebs pers. comm.). However, it is unknown whether predators still negatively influenced reproduction rates since there was no treatment that excluded predators from ground squirrel populations.

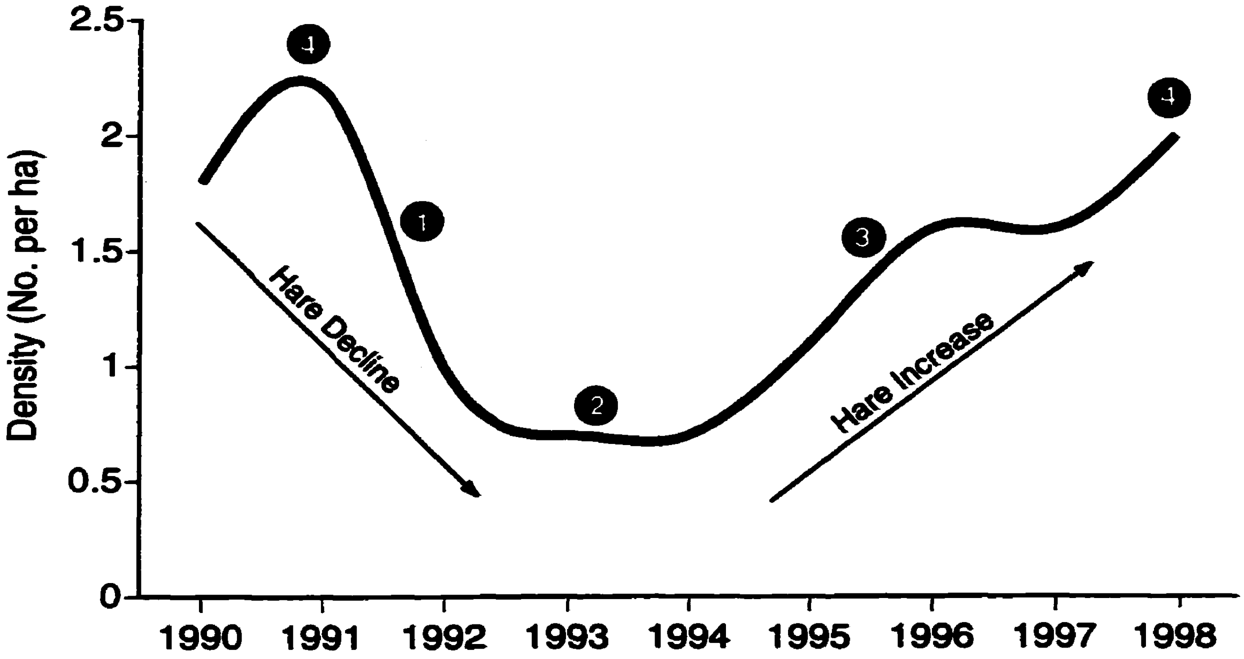


Figure 5.1 A schematic summary of the changes in arctic ground squirrel populations during a complete snowshoe hare cycle from 1990 to 1998. **Decline Phase (●):** As snowshoe hares declined, arctic ground squirrel populations declined because of intense, density-independent predation and possibly because of by density-independent sublethal effects of predators on reproduction. These effects reduced the population limit towards the low. **Low Phase (●):** Populations were limited by an interaction between food and predators. **Increase Phase (●):** When hares increased, predation on ground squirrels was nearly absent, and populations increased through density-dependent reproduction and decreased through density-dependent overwinter mortality. However, the sublethal effects of predators were still operating to limit reproductive rate and thus to reduce the maximum rate of increase. **Peak Phase (●):** The maximum density of ground squirrel was limited primarily by density-dependent overwinter mortality through competition for food resources.

A model combining density dependence and density independence

The population dynamics of the arctic ground squirrel are presented in Figure 5.2 as a model of density-dependent and density-independent rates adapted from theoretical models presented in Sinclair and Pech (1996). Production rate *P*, represents the number of young produced per capita. This parameter represents weaning rate in my model and declines as population density increases. This model assumes that litter size, pre- or post-partum, is constant across all densities. However, there is variation in *P* shown by shaded areas that represent density-independent fluctuations in *P*. For arctic ground squirrels, this variation could be caused by the interactive effects of food and predators on weaning rates (Karels et al. 2000) or possibly by the effects of winter snowpack influencing the body condition of squirrels emerging in spring which in turn influences reproduction. There are two sources of mortality, predation (m_1) and death during hibernation (m_2). Predation mortality (m_1) occurs at constant rate across all densities and effectively lowers the production curve by removing a constant proportion of individuals from the population. During a cyclic fluctuation of snowshoe hares and their predators, m_1 fluctuates from a low rate during the increase and peak phases of the hare cycle, producing the upper production curve, to a high rate during the decline and early low phases of the hare cycle, thus producing the lower production curve.

Hibernation mortality (m_2) is represented by the solid line in Figure 5.2 and occurs at a rate that increases as fall population density increases. During the increase and high phases of the hare cycle, when the rate of predation on ground squirrels is lowest, m_2 intersects the upper production curve. During the decline and low phases of the hare cycle, when the rate of predation on ground squirrels is greatest, m_2 intersects the lower production curve. In a simpler model, these points would represent the equilibrium densities at the increase-high phase (i.e k_1) and at decline-low phases (i.e k_2,) where births equal deaths and the population is stable. However, because there is variation in P, there is also variation in k that becomes a 'range of k'. This range represents the possible range of densities during the cyclic peak of ground squirrel numbers k_1 and the cyclic low of ground squirrels numbers k_2. However, m_1 does not spontaneously jump from one extreme to another but changes gradually from weak to strong and back to weak rates of predation thus producing a range of k that slides from k_1 to k_2 and back to k_1.during an entire hare cycle from the increase phase to the decline phase and back to the increase phase.

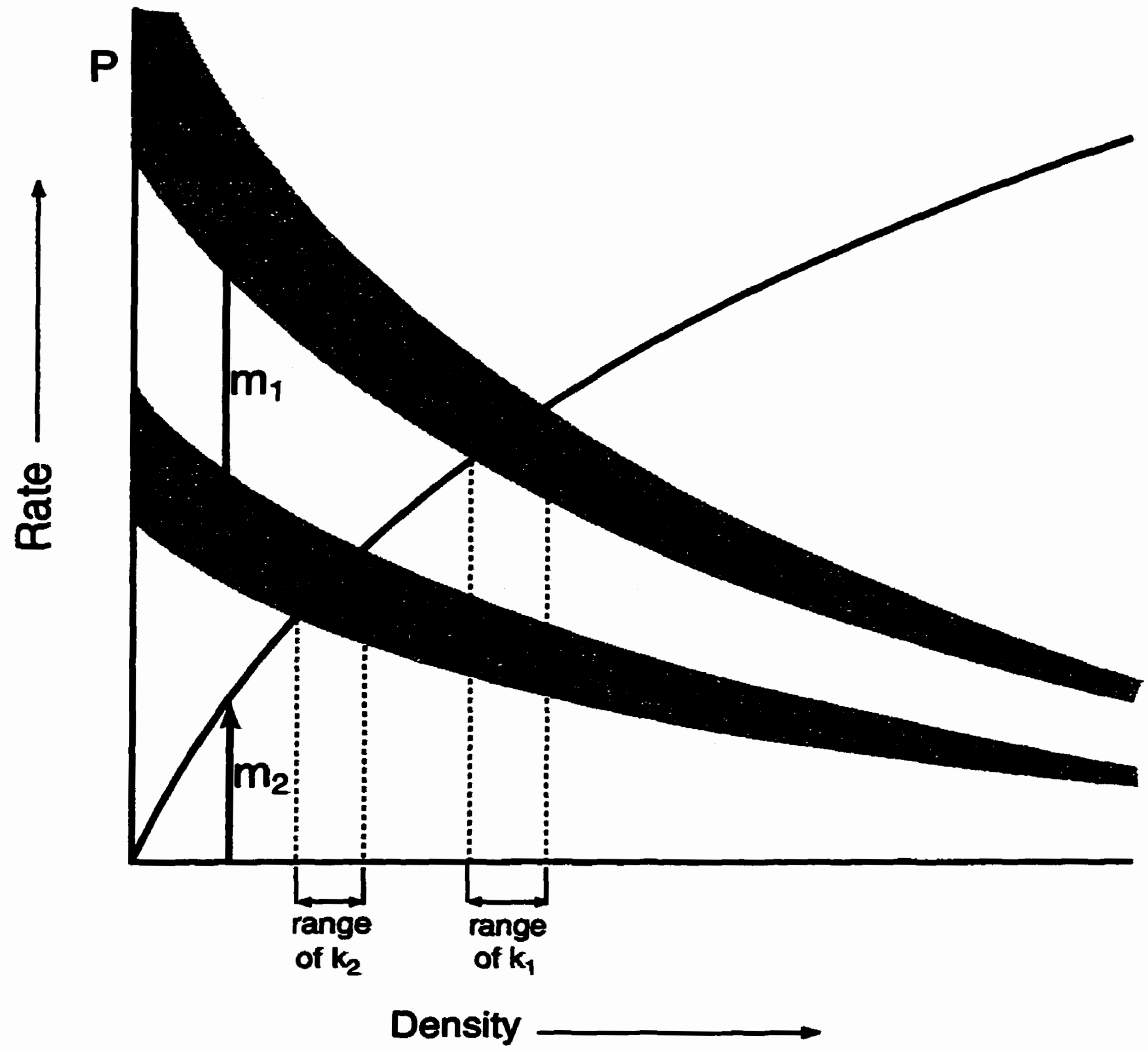


Figure 5.2 Conceptual model of density-dependent production P and density-dependent overwinter mortality m_2 for arctic ground squirrels (adapted from Sinclair and Pech 1996). Mortality m_1 (predation) is density independent and reduces net production during the summer. m_1 fluctuates during the course of the snowshoe hare cycle with low predation during the increase phase of snowshoe hares producing the upper production curve and intense predation during the decline phase of snowshoe hares producing the lower production curve. Values k_1 and k_2 representing the range of equilibrium densities where production equals deaths during low predation during the increase of hares and during the intense predation during the decline phase of hares, respectively. Ranges within k-values are produced by density-independent variation in weaning rates (grey area) owing to fluctuation in sublethal effects of predators and/or variation in winter conditions (snow depth). In this model k is essentially a range of equilibrium densities that continuously slides from the upper range (k_1) of densities during the increase phase of the hare cycle when predation on ground squirrels is low to the lower range (k_2) of densities at the decline phase of hares when predation on ground squirrels is intense.

Questions and future research directions

My research has answered a number of key questions in the population ecology of arctic ground squirrels, but it has also served to raise others and these I outline below:

The role of predators in population regulation

It is plausible that had the termination of the Kluane project been timed to coincide with the decrease phase in hares rather than with the increase phase, the results presented in Chapter 2 would have been different. If my study was conducted during the decline phase, predators may have played a more important role in returning ground squirrel populations back to control densities than during the increase phase. The high densities of squirrels on the experimental treatments may have attracted more predators or encouraged individual predators to concentrate their efforts on that site. Rohner and Krebs (1998) experimentally tested the response of great horned owls (*Bubo virginianus*) to 'hot spots' of high snowshoe hare densities created by the experimental manipulations of food and mammalian predators at Kluane. 'Hot spots' within owl territories did not alter the space use of those owls and 'hot spots' did not attract territorial and non-territorial owls. They concluded that territorial behaviour limits growth and aggregation of predators at intermediate spatial scales. However, mammalian predators may react differently to 'hot spots'. O'Donoghue et al. (1998) found that lynx (*Lynx canadensis*) and coyotes (*Canis latrans*) concentrated their hunting in areas of higher hare abundance. During the final winter of the Kluane Project, Hodges et al. (1999) found that a single coyote, which found its way into the predator exclosure + food treatment, accounted for at least 39.3% of the total predation on that site in comparison to control areas where coyotes accounted for 22% of the total predation in that same winter. Therefore, mammalian predators may be capable of regulating ground squirrels if they respond in a density-dependent manner.

If my study had coincided with the hare decline, it would have been possible to determine the role of sublethal effects of predators on ground squirrel population regulation. Would sublethal effects of predators on reproduction in squirrels be density-dependent or would sublethal effects be constant across all densities? Density perturbation studies could be designed with manipulation of predators to test how squirrels at different population densities respond to the presence and absence of predators.

Overwinter survival

I found that strength of density dependence in overwinter survival remained similar over two winters. However, it is too early to assume that this relationship is constant at all times but rather that there is variation in density-dependent overwinter survival in the same way as there is variation in the density-dependent weaning rate. Changes in snowpack or overwinter temperatures could change the relationship between overwinter survival and population density.

The role of essential fatty acids in population dynamics

Although food has major limiting and regulating effects on ground squirrel populations, it is unknown what component of the dietary requirements of ground squirrels limits both their reproduction in summer and their survival over winter. Are essential fatty acids limiting in the food supplies of ground squirrels in natural populations? If they are limiting, what are the implications for life-history strategies of organisms attempting to obtain the required quantities? Do fatty acids limit the rate of reproduction and of overwinter survival? Is there a direct relationship between reproduction and overwinter survival mediated through essential fatty acids? These questions could be easily addressed with careful food supplementation experiments as have been conducted in laboratory experiments (Geiser and Kenagy 1987; Frank 1992; Geiser et al. 1992; Thorp et al. 1994; Frank and Storey 1995). Factorial designs consisting of high and low levels of essential fatty acids and high and low levels of proteins could tease out the relative contribution of these nutrients to reproduction and survival in natural populations of ground squirrels to address these important issues.

Snowpack and reproduction

Snow accumulation over winter hibernacula appeared to influence the rate of mass loss in ground squirrels which may impact the residual fat stores in spring that are supplemental to reproduction. What would be required to test this is a direct manipulation of snow depth over hibernacula during winter. Snow could be removed or added over hibernating ground squirrels to test the relationship between snow depth and reproductive performance during the subsequent breeding season.

Mechanism of sublethal effects of predators

It is unknown how predators negatively influence reproduction in ground squirrels. Predators may cause changes in the foraging behaviour of their prey such that foraging rate is reduced when predators are abundant and this results in declines in squirrel condition and fecundity as proposed for snowshoe hares by Hik (1995). Alternatively, predators may influence their prey through effects of chronic stress as shown for snowshoe hares by Boonstra et al. (1998). Boonstra et al. (1998) showed that during the decline phase of the snowshoe hare cycle when predators were abundant, hares experienced severe stress effects that were associated with poor reproduction. It is possible that both mechanisms operate simultaneously, but this remains to be tested.

Literature Cited

Agrell, J., J. W. Wolff, and H. Ylönen. 1998. Counter-strategies to infanticide in mammals: costs and consequences. Oikos **83**: 507-517.

Andersen, D. C., K. B. Armitage, and R. S. Hoffmann. 1976. Socioecology of marmots: female reproductive strategies. Ecology **57**: 552-560.

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.

Anufriev, A. I., and A. K. Akhremenko. 1990. Energetic cost of hibernation of the Arctic ground squirrel. The Soviet Journal of Ecology **21**: 279-283.

Arcese, P., and J. N. M. Smith. 1988. Effects of population density and supplemental food on reproduction in song sparrows. Journal of Animal Ecology **57**: 119-136.

Armitage, K. B., J. F. Downhower, and G. E. Svendsen. 1976. Seasonal changes in weights of marmots. American Midland Naturalist **96**: 36-51.

Arnold, W. 1990. The evolution of marmot sociality: II Costs and benefits of joint hibernation. Behavioural Ecology and Sociobiology **27**: 239-246.

Arnold, W. 1993. Energetics of social hibernation. 65-80 *in* C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, editors, Life in the cold. Ecological, physiological and molecular mechanisms. Westview Press, Boulder, Colorado,

Arnold, W. 1995. Social behaviour and telemetric assessment of thermoregulation in hibernating marmots. 395-411 *in* E. Alleva et al., editor, Behavioural brain research in naturalistic and semi-naturalistic settings. Kluwer Academic, Dordrecht,

Arnold, W., G. Heldmaier, S. Ortmann, H. Pohl, T. Ruf, and S. Steinlechner. 1991. Ambient temperatures in hibernacula and their energetic consequences for alpine marmots (*Marmota marmota*). Journal of Thermal Biology **4**: 223-226.

Banfield, A. W. F. 1974. The Mammals of Canada. University of Toronto Press, Toronto and Buffalo.

Barash, D. P. 1974. The social behavior of the hoary marmot (*Marmota caligata*). Animal Behaviour **22**: 256-261.

Barnes, B. M. 1989. Freeze avoidance in a mammal: body temperatures below 0 ° C. Science **244**: 1593-1595.

Barnes, B. M., and D. Ritter. 1993. Patterns of body temperature change in hibernating arctic ground squirrels. *in* C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, editors, Life in the cold: ecological, physiological, and molecular mechanisms. Westview Press, Boulder, Colorado,

Batzli, G. O., and S. T. Sobaski. 1980. Distribution, abundance, and foraging patterns of ground squirrels near Atkasook, Alaska. Arctic and Alpine Research **12**: 501-510.

Bazhan, N. M., E. N. Makarova, and T. V. Yakovleva. 1996. Deprivation of food during pregnancy and reproduction in the water vole (*Arvicola terrestris*). Journal of Mammalogy **77**: 1078-1084.

Ben-David, M., C. J. McColl, R. Boonstra, and T. J. Karels. 1999. ^{15}N signatures do not reflect body condition in arctic ground squirrels. Canadian Journal of Zoology **77**: 1373-1378.

Blumstein, D. T., and W. Arnold. 1998. Ecology and social behavior of golden marmots (*Marmota caudata aurea*). Journal of Mammalogy **79**: 873-886.

Blumstein, D. T., and J. M. Foggin. 1997. Effects of vegetative variation on weaning success, overwinter survival, and social group density in golden marmots (*Marmota caudata aurea*). Journal of Zoology **243**: 57-69.

Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecological Monographs **79**: 371-394.

Boonstra, R., and C. J. McColl. 2000. Contrasting stress response of male arctic ground squirrels and red squirrels. Journal of Experimental Zoology **286**: 390-404.

Boulanger, J., and C. J. Krebs. 1994. Comparison of capture-recapture estimators of snowshoe hare populations. Canadian Journal of Zoology **72**: 1800-1807.

Boutin, S., C. J. Krebs, R. Boonstra, M. R. T. Dale, S. J. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, R. Turkington, M. Blower, A. Byrom, F. I. Doyle, C. Doyle, D. Hik, L. Hofer, A. Hubbs, T. Karels, D. L. Murray, V. Nams, M. O'Donoghue, C. Rohner, and S. Schweiger. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. Oikos **74**: 69-80.

Boyd, D. W. 1979. Degree days: the different types. 138, National Research Council of Canada, Division of Building Research, Building Research Note.

Brown, R. J. E. 1967. Permafrost in Canada. , Geological Survey, Canada.

Bryant, A. A. 1998. Metapopulation ecology of Vancouver Island marmots. PhD Thesis. University of Victoria, Victoria, British Columbia.

Buck, C. L., and B. M. Barnes. 1999a. Annual cycle of body composition and hibernation in free-living arctic ground squirrels. Journal of Mammalogy **80**: 430-442.

Buck, C. L., and B. M. Barnes. 1999b. Temperatures of hibernacula and changes in body composition of arctic ground squirrels over winter. Journal of Mammalogy **80**: 1264-1276.

Byrom, A. E., T. Karels, C. J. Krebs, and R. Boonstra. 2000. Experimental manipulation of predation and food for arctic ground squirrels in the boreal forest. Canadian Journal of Zoology **in press.**

Byrom, A. E., and C. J. Krebs. 1999. Natal dispersal of juvenile arctic ground squirrels in the boreal forest. Canadian Journal of Zoology **77**: 1048-1059.

Byth, K. 1982. On robust distance-based intensity estimators. Biometrics **38**: 127-135.

Campbell, M. T., and N. A. Slade. 1995. The effect of maternal mass on litter size and offspring survival in the hispid cotton rat (*Sigmodon hispidus*). Canadian Journal of Zoology **73**: 1333-140.

Cappuccino, N. 1995. Novel approaches to the study of population dynamics. 3-16 *in* N. Cappucino, editor, Population dynamics : new approaches and synthesis. Academic Press, Inc., London,

Cappuccino, N., and S. Harrison. 1996. Density-perturbation experiments for understanding population regulation. 53-64 *in* R. B. Floyd, A. W. Sheppard, and P. J. De Barro, editors, Frontiers of population ecology. CSIRO Publishing, Melbourne,

Carl, E. A. 1971. Population control in arctic ground squirrels. Ecology **52**: 395-413.

Caughley, G. 1994. Direction in conservation biology. Journal of Animal Ecology **63**: 215-244.

Caughley, G., and A. R. E. Sinclair. 1994. Wildlife ecology and management. Blackwell Science, Cambridge.

Chappel, M. A. 1981. Standard operative temperature and cost of thermoregulation in the arctic ground squirrel. Oecologia **49**: 397-403.

Chitty, D. 1967. The natural selection of self-regulatory behaviour in animal populations. Proceedings of the Ecological Society of Australia **2**: 51-78.

Choquenot, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. Ecology **72**: 805-813.

Chouinard, P. Y., L. Coreau, D. M. Barbano, L. E. Metzger, and D. E. Bauman. 1999. Conjugated linoleic acids alter milk fatty acid composition and inhibit milk fat secretion in dairy cows. Journal of Nutrition **129**: 1579-1584.

Christensen, R. 1997. Log-linear models and logistic regression. Springer-Verlag, New York.

Christian, J. J., and D. E. Davis. 1964. Endocrines, behavior, and population. Science **146**: 1550-1560.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1986. Great expectations: dominance, breeding success and offspring sex ratios in red deer. Animal Behaviour **34**: 460-471.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1989. Fitness costs of gestation and lactation in wild mammals. Nature **337**: 260-262.

Clutton-Brock, T. H., D. Gaynor, G. M. McIlrath, A. D. C. MacColl, R. Kansky, P. Chadwick, M. Manser, J. D. Skinner, and P. N. Brotherton. 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. Journal of Animal Ecology **68**: 672-683.

Clutton-Brock, T. H., I. R. Stevenson, P. Marrow, A. D. MacColl, A. I. Houston, and M. M. McNamara. 1996. Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. Journal of Animal Ecology **65**: 675-689.

Crête, M., and R. Courtois. 1997. Limiting factors might obscure population regulation of moose (Cervidae: *Alces alces*) in unproductive boreal forests. Journal of Zoology **242**: 765-781.

Department of Public Works and U.S. Department of Transportation Federal Highway Administration. 1977. Shakwak Highway improvement, British Columbia and Yukon Territory, Canada. Department of Public Works, Ottawa, Ontario, Canada.

Dobson, F. S. 1990. Environmental influences on infanticide in Columbian ground squirrels. Ethology **84**: 3-14.

Dobson, F. S. 1995. Regulation of population size: evidence from Columbian ground squirrels. Oecologia **102**: 44-51.

Dobson, F. S., and J. D. Kjelgaard. 1985a. The influence of food resources on life history in Columbian ground squirrels. Canadian Journal of Zoology **63**: 2105-2109.

Dobson, F. S., and J. D. Kjelgaard. 1985b. The influence of food resources on population dynamics in Columbian ground squirrels. Canadian Journal of Zoology **63**: 2095-2104.

Dobson, F. S., and G. R. Michener. 1995. Maternal traits and reproduction in Richardson's ground squirrels. Ecology **76**: 851-862.

Dobson, F. S., T. S. Risch, and J. O. Murie. 1999. Increasing returns in the life history of Columbian ground squirrels. Journal of Animal Ecology **68**: 73-86.

Doughty, P., and R. Shine. 1998. Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). Ecology **79**: 1073-7083.

Feltmate, B. W., and D. D. Williams. 1991. Evolution of predator-induced stress on field populations of stoneflies (Plecoptera). Ecology **72**: 1800-1806.

Festa-Bianchet, M., J.-M. Gaillard, and J. T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist **152**: 367-379.

Festa-Bianchet, M., and W. J. King. 1991. Effects of litter size and populations dynamics on juvenile and maternal survival in Columbian ground squirrels. Journal of Animal Ecology **60**: 1077-1090.

Florant, G. L. 1998. Lipid metabolism in hibernators: the importance of essential fatty acids. American Zoologist **38**: 331-340.

Florant, G. L., H. S. Ameednuddin, and D. A. Rintoul. 1993. The effect of a low essential fatty acid diet on hibernation in marmots. American Journal of Physiology **264**: R747-R753.

Florant, G. L., L. C. Nuttle, D. E. Mullinex, and D. A. Rintoul. 1990. Plasma and white adipose tissue lipid composition in marmots. American Journal of Physiology **258**: R1123-1131.

Francois, C. A., S. L. Connor, R. C. Wander, and W. E. Connor. 1998. Acute effects of dietary fatty acids on the fatty acids of human milk. American Journal of Clinical Nutrition **67**: 301-308.

Frank, C. L. 1992. The influence of dietary fatty acids on hibernation by Golden-mantled ground squirrels (*Spermophilus lateralis*). Physiological Zoology **65**: 906-920.

Frank, C. L. 1994. Polyunsaturate content and diet selection by ground squirrels (*Spermophilus lateralis*). Ecology **75**: 458-463.

Frank, C. L., E. S. Dierenfeld, and K. B. Storey. 1998. The relationship between lipid peroxidation, hibernation, and food selection in mammals. American Zoologist **38**: 341-349.

Frank, C. L., and K. B. Storey. 1995. The optimal depot fat composition for hibernation by gold-mantled ground squirrels (*Spermophilus lateralis*). Journal of Comparative Physiology B **164**: 536-542.

Gagnon, J., J. Roth, B. Finzer, R. Hofmann, K. Haycock, J. Simpson, and D. Feldman. 1991. SuperANOVA. , Abacus Concepts, Inc., Berkely, California.

Geiser, F. 1991. The effect of unsaturated and saturated dietary lipids on the pattern of daily torpor and the fatty acid composition of tissues and membranes of the deer mouse *Peromyscus maniculatus*. Journal of Comparative Physiology B **161**: 590-597.

Geiser, F., and G. J. Kenagy. 1987. Polyunsaturated lipid diet lengthens torpor and reduces body temperature in a hibernator. American Journal of Physiology **252**: R897-901.

Geiser, F., and G. J. Kenagy. 1993. Dietary fats and torpor patterns in hibernating ground squirrels. Canadian Journal of Zoology **71**: 1182-1186.

Geiser, F., B. Stahl, and R. P. Learmonth. 1992. The effect of dietary fatty acids on the pattern of torpor in a marsupial. Physiological Zoology **65**: 1236-1245.

Geiser, G. 1990. Influence of polyunsaturated and saturated dietary lipids on adipose tissue, brain and mitochondiral membrane fatty acid compostiion of a mammalian hibernator. Biochim Biophys Acta **1046**: 159-166.

Gerhart, K. L., D. E. Russell, D. Van De-Wetering, R. G. White, and R. D. Cameron. 1997. Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactation infertility. Journal of Zoology (London) **242**: 17-30.

Green, J. E. 1977. Population regulation and annual cycles of activity and dispersal in the Arctic ground squirrel. MSc Thesis. University of British Columbia.

Hackländer, K., and W. Arnold. 1999. Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). Behavioral Ecology **5**: 592-597.

Hansen, R. M. 1975. Foods of the Hoary marmot on Kenai Peninsula, Alaska. American Midland Naturalist **94**: 348-353.

Hansen, R. M., and M. K. Johnson. 1976. Stomach content weight and food selection by Richardson ground squirrels. Journal of Mammalogy **57**: 749-751.

Hansen, R. M., and D. N. Ueckert. 1970. Dietary similarity of some primary consumers. Ecology **51**: 640-648.

Hare, J. F. 1991. Intraspecific killing of preweaned young in the Columbian ground squirrel, *Spermophilus columbianus*. Canadian Journal of Zoology **69**: 797-800.

Hare, J. F., and J. O. Murie. 1992. Manipulation of litter size reveals no cost of reproduction in Columbian ground squirrels. Journal of Mammalogy **73**: 449-454.

Harrison, S., and N. Cappuccino. 1995. Using density-manipulation experiments to study population regulation. 131-147 *in* N. Cappuccino and P. W. Price, editors, Population dynamics: new approaches and synthesis. Academic Press, Inc., London, Harwood, H. J., and R. P. Geyer. 1964. Biology data book. Federation of American Societies for Experimental Biology, Washington, D. C., USA.

Henry, C. J., A. Ghusain-Choueiri, and P. R. Payne. 1996. Protein utilization, growth and survival in essential-fatty-acid-deficient rats. British Journal of Nutrition **75**: 237-248.

Hik, D. S. 1995. Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshoe hares. Wildlife Research **22**: 115-129.

Hill, V. L., and G. L. Florant. 1999. Patterns of fatty acid compostion in free-ranging yellow-bellied marmots (*Marmot flaviventris*) and their diet. Canadian Journal of Zoology **77**: 1494-1503.

Hock, R. J. 1960. Seasonal variations in physiologic functions of Arctic ground squirrels and bears. Bulletin: Museum of Comparative Zoology **124**: 155-171.

Hodges, K. E. 1998. Snowshoe hare demography and behaviour during a cyclic population low phase. PhD Thesis. University of British Columbia, Vancouver, British Columbia.

Hodges, K. E., C. J. Krebs, and A. R. E. Sinclair. 1999. Snowshoe hare demography during a cyclic popualtion low. Journal of Animal Ecology **68**: 581-594.

Holmes, W. G. 1979. Social behavior and foraging strategies of hoary marmots (*Marmota caligata*) in Alaska. PhD Thesis. University of Washington, Seattle.

Holyoak, M. 1994. Appropriate time scales for identifying lags in density-dependent processes. Journal of Animal Ecology **63**: 479-483.

Hoogland, J. L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. University of Chicago Press, Chicago.

Hosmer, D. W. J., and S. Lemeshow. 1989. Applied logistic regression. Wiley, New York.

Howard, L. O., and W. F. Fiske. 1911. The importation into the United States of the parasites of the gipsy moth and the brown-Tail moth: A report of progress with some consideration of previous and concurrent efforts of this kind. Bulletin, United States Department of Agriculture, Bureau of Entomology **91**: 105-109.

Howell, A. H. 1938. Revision of the North American ground squirrels, with a classification of the North American Sciuridae. 56, United States Department of Agriculture.

Hubbs, A., and R. Boonstra. 1998. Effects of food and predators on home range sizes of Arctic ground squirrels (*Spermophilus parryiil*). Canadian Journal of Zoology **76**: 592-596.

Hubbs, A. H., and R. Boonstra. 1997. Population limitation in Arctic ground squirrels: effects of food and predation. Journal of Animal Ecology **66**: 527-541.

Huber, S., E. Millesi, M. Walzl, J. Dittami, and W. Arnold. 1999. Reproductive effort and costs of reproduction in female European ground squirrels. Oecologia **121**: 19-24.

Humphries, M. M., and S. Boutin. 1996. Reproductive demands and mass gains: a paradox in female red squirrels (*Tamiasciurus hudsonicus*). Journal of Animal Ecology **65**: 332-338.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**: 187-211.

Jenkins, K. J., and J. K. G. Kramer. 1985. Influence of low linoleic and linolenic acids in milk replacer on calf performance and lipids in blood plasma, heart, and liver. Journal of Dairy Science **69**: 1374-1386.

Karels, T. J., and R. Boonstra. 1999. Predation risk and the selection of burrow sites by Arctic ground squirrels. Proceedings of the Royal Society of London Series B **266**: 2117-2123.

Karels, T. J., A. E. Byrom, R. Boonstra, and C. J. Krebs. 2000. The interactive effects of food and predators on reproduction and overwinter survival of arctic ground squirrels. Journal of Animal Ecology **69**: 235-247.

Kenagy, G. J. 1987. Energy allocation for reproduction in the golden-mantled ground squirrel. Symposium of the Zoological Society of London **57**: 259-273.

Kiell, D. J., and J. S. Millar. 1980. Reproduction and nutrient reserves of arctic ground squirrels. Canadian Journal of Zoology **58**: 416-421.

King, W. J., M. Festa-Bianchet, and S. E. Hatfield. 1991. Determinants of reproductive success in female Columbian ground squirrels. Oecologia **86**: 528-534.

Koskela, E., T. Mappes, and H. Ylõnen. 1999. Experimental manipulation of breeding density and litter size: effects on reproductive success in the bank vole. Journal of Animal Ecology **68**: 513-521.

Krebs, C. J. 1991. The experimental paradigm and long-term population studies. Ibis **133**: 3-8.

Krebs, C. J. 1994. Ecology: The experimental analysis of distribution and abundance. University of Chicago Press, Chicago.

Krebs. C. J. 1995. Two paradigms of population regulation. Journal of Wildlife Research **22**: 1-10.

Krebs, C. J. 1998. Ecological Methodology. Exeter Software, Setauket, New York.

Krebs, C. J. 1999. Ecological methodology. Benjamin/Cummings, Menlo Park.

Krebs, C. J., R. Boonstra, S. Boutin, M. Dale, S. Hannon, K. Martin, A. R. E. Sinclair, J. N. M. Smith, and R. Turkington. 1992. What drives the snowshoe hare cycle in Canada's Yukon? 886-896 *in* D. R. McCullough and R. H. Barrett, editors, Wildlife 2001: Populations. Elsevier Science Publications, London and New York, Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science **269**: 1112-1115.

Lacey, E. A. 1991. Reproductive and dispersal strategies of male Arctic ground squirrels (*Spermophilus parryii plesius*). PhD Thesis. University of Michigan, Ann Arbor, Michigan.

Lacey, E. A., J. R. Wieczorek, and P. K. Tucker. 1997. Male mating behaviour and patterns of sperm precedence in Arctic ground squirrels. Animal Behaviour **53**: 565-779.

Lehninger, A. L. 1982. Principles of Biochemistry. Worth, New York, New York, USA.

Leirs, H., N. C. Stenseth, J. D. Nichols, J. E. Hines, R. Verhagen, and W. Verheyen. 1997. Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. Nature **389**: 176-180.

Lenihan, C., and D. Van Vuren. 1996. Growth and survival juvenile yellow-bellied marmots (*Marmota flaviventris*). Canadian Journal of Zoology **74**: 297-302.

Lincoln, B. J. 1972. Behavior study of the Arctic ground squirrel, *Citellus parryi plesius*. Icefield Ranges Research Project Science Results **3**: 245-253.

Lundy, K. J., P. G. Parker, and Z. Zahavi. 1998. Reproduction by subordinates in cooperatively breeding Arabian babblers is uncommon but predictable. Behavioral Ecology & Sociobiology **43**: 173-180.

Majak, W., W. J. Keller, Z. Duan, D. Munro, R. A. Smith, A. M. Davis, and R. T. Ogilvie. 1994. Alkaloid distribution in two species of *Lupinus* in central British Columbia. Phytochemistry **36**: 883-885.

Mallory, F. F., and T. D. Heffernan. 1987. Floristic modification of low arctic tundra by the Arctic ground squirrel, *Spermophilus parryii*. Canadian Field-Naturalist **101**: 388-391.

Mallory, M. L., D. K. McNicol, and P. J. Weatherhead. 1994. Habitat quality and reproductive effort of common goldeneyes nesting near Sudbury, Canada. Journal of Wildlife Management **58**: 552-560.

Marchand, P. J. 1991. Life in the cold. An introduction to winter ecology. University Press of New England, Hanover and London.

Matos, D. M. S., R. P. Freckleton, and A. R. Watkinson. 1999. The role of density dependence in the population dynamics of a tropical palm. Ecology **80**: 2635-2650.

Mayer, W. V. 1953. Some aspects of the ecology of the barrow ground squirrel, *Citellus parryi barrowensis*. Stanford University publications University Series Biological Sciences **11**: 48-55.

Mayer, W. V. 1955. The protective value of the burrow system to the hibernating arctic ground squirrel, *Spermophilus undulatus*. Anatomical Record **122**: 437-438.

Mayer, W. V., and E. T. Roche. 1954. Developmental patterns in the Barrow ground squirrel, *Spermophilus undulatus barrowensis*. Growth **18**: 53-69.

McCullough, D. R. 1999. Density dependence and life-history strategies of ungulates. Journal of Mammalogy **80**: 1130-1146.

McLean, I. G. 1981. Social ecology of the arctic ground squirrel. PhD Thesis. The University of Alberta, Edmonton.

McLean, I. G. 1983. Paternal behaviour and killing of young in arctic ground squirrels. Animal Behaviour **31**: 32-44.

McLean, I. G. 1985. Seasonal patterns and sexual differences in the feeding ecology of arctic ground squirrels (*Spermophilus parryiii plesius*). Canadian Journal of Zoology **63**: 1298-1301.

McLean, I. G., and A. J. Towns. 1981. Differences in weight changes and the annual cycle of male and female arctic ground squirrels. Arctic **34**: 249-254.

McNamara, J. M., and A. I. Houston. 1996. State-dependent life histories. Nature **380**: 215-221.

McNamara, J. P. 1995. Role and regulation of metabolism in adipose tissue during lactation. Nutritional Biochemistry **6**: 120-129.

Mead, J. F., R. Alfin-Slater, D. Howton, and G. Popjak. 1986. Lipds: chemistry, biochemistry, and nutrition. Plenum, New York, New York, USA.

Menkens, G. E., and S. H. Anderson. 1988. Estimation of small-mammal population size. Ecology **69**: 1952-1959.

Michener, D. R. 1974. Annual cycle of activity and weight changes in Richardson's ground squirrel, *Spermophilus richardsonii*. Canadian Field Naturalist **88**: 409-413.

Michener, G. R. 1989. Reproductive effort during gestation and lactation by Richardson's ground squirrels. Oecologia **78**: 77-86.

Michener, G. R. 1992. Sexual differences in over-winter torpor patterns of Richardson's ground squirrels in natural hibernacula. Oecologia **89**: 397-406.

Michener, G. R. 1993. Sexual differences in hibernaculum contents of Richardson's ground squirrels: males store food. 109-118 *in* C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, editors, Life in the cold: ecological, physiological and molecular mechanisms. Westview Press, Boulder, Colorado,

Millar, J. S. 1972. Timing of breeding of pikas in southwestern Alberta. Canadian Journal of Zoology **50**: 665-669.

Millar, J. S. 1977. Adaptive features of mammalian reproduction. Evolution **31**: 370-386.

Millesi, E., A. M. Strijkstra, I. E. Hoffman, J. P. Dittami, and S. Daan. 1999. Sex and age differences in mass, morphology, and annual cycle in European ground squirrels, *Spermophilus citellus*. Journal of Mammalogy **80**: 218-213.

Morris, D. W. 1992. Optimal brood size: tests of alternative hypotheses. Evolution **46**: 1848-1861.

Morris, D. W. 1998. State-dependent optimization of litter size. Oikos **83**: 518-528.

Morton, M. L., and P. W. Sherman. 1978. Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. Canadian Journal of Zoology **56**: 2578-2590.

Murdoch, W. M., and R. M. Nisbet. 1996. Frontiers of population ecology. 31-43 *in* R. B. Floyd, A. W. Sheppard, and P. J. De Barro, editors, Frontiers of population ecology. CSIRO Publishing, Melbourne,

Murdoch, W. W. 1970. Population regulation and population inertia. Ecology **51**: 497-502.

Murdoch, W. W. 1994. Population regulation in theory and practice. Ecology **75**: 271-287.

Murdoch, W. W., and S. J. Walde. 1989. Analysis of insect population dynamics. 113-140 *in* P. J. Grubb and J. B. Whittaker, editors, Towards a more exact ecology. Blackwell, Oxford,

Murie, J. O., and D. A. Boag. 1984. The relationship of body weight to overwinter survival in Columbian ground squirrels. Journal of Mammalogy **65**: 688-690.

Murie, J. O., and F. S. Dobson. 1987. The costs of reproduction in female Columbian ground squirrels. Oecologia **73**: 1-6.

Murray, B. G. J. 1994. On density dependence. Oikos **69**: 520-523.

Murray, B. J., Jr. 1999. Can the population regulation controversy be buried and forgotten? Oikos **84**: 148-152.

Murray, D. L., and S. Boutin. 1991. The influence of snow on lynx and coyote movements in the southwestern Yukon: Does morphology affect behaviour? Oecologia **88**: 463-469.

Nadler, C. F., and R. S. Hoffmann. 1977. Patterns of evolution and migration in the arctic ground squirrel, *Spermophilus parryii* (Richardson). Canadian Journal of Zoology **55**: 748-758.

Neuhaus, P., R. Bennett, and A. Hubbs. 1999. Effects of a late snowstorm and rain on survival and reproductive success in Columbian ground squirrels (*Spermophilus columbianus*). Canadian Journal of Zoology **77**: 879-884.

Neuringer, M., G. J. Anderson, and W. E. Connor. 1988. The essentiality of n - 3 fatty acids for the development and function of retina and brain. Annual Review of Nutrition **8**: 517-41.

Newton, I. 1998. Population limitation in birds. Academic Press Inc., San Diego, CA, USA.

Nicholson, A. J. 1933. The balance of animal populations. Journal of Animal Ecology **2**: 132-178.

O'Donoghue, M., S. Boutin, C. J. Krebs, D. L. Murray, and E. J. Hofer. 1998. Behavioural responses of coyotes and lynx to the snowshoe hare cycle. Oikos **82**: 169-183.

Oksanen, L., and P. Lundberg. 1995. Optimization of reproductive effort and foraging time in mammals: the influence of resource level and predation risk. Evolutionary Ecology **9**: 45-56.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference for capture data from closed populations. Wildlife Monographs **62**: 1-135.

Panter, K. E., D. R. Gardner, and R. J. Molyneux. 1994. Comparison of toxic and teratogenic effects of *Lupinus formosus, L. arbustus* and *L. caudatus* in goats. Journal of Natural Toxins 3: 83-93.

Phillips, J. A. 1984. Environmental influences on reproduction in the Golden-mantled ground squirrel. 108-141 *in* J. O. Murie and G. R. Michener, editors, The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality. University of Nebraska, Lincoln and London,

Pollock, K. H., J. D. Nichols, C. Browne, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs **107**: 1-97.

Pond, C. M. 1998. The fats of life. Cambridge University Press, Cambridge.

Rafael, J., J. Patzelt, and I. Elmadfa. 1988. Effect of dietary linoleic acid and essential fatty acid deficiency on resting metabolism, nonshivering thermogenesis and brown adipose tissue in the rat. Journal of Nutrition **114**: 255-262.

Rafael, J., J. Patzelt, H. Schafer, and I. Elmadfa. 1984. The effect of essential fatty acid deficiency on basal respiration and function of liver mitochondria in rats. Journal of Nutrition **114**: 255-262.

Rampton, V. N. 1981. Surficial materials and landforms of Kluane National Park, Yukon Territory. Geological Survey of Canada.

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos **44**: 257-267.

Riddington, R., and A. G. Gosler. 1995. Differences in reproductive success and parental qualities between habitats in the Great Tit *Parus major*. Ibis **137**: 371-378.

Rieger, J. F. 1996. Body size, litter size, timing of reproduction, and juvenile survival in the Uinta ground squirrel, *Spermophilus armatus*. Oecologia **107**: 463-468.

Risch, T. S., F. S. Dobson, and J. O. Murie. 1995. Is mean litter size the most productive? a test in Columbian ground squirrels. Ecology **76**: 1643-1654.

Rodenhouse, N. L., T. W. Sherry, and R. T. Holmes. 1997. Site-dependent regulation of population size: a new synthesis. Ecology **78**: 2025-2042.

Roff, D. A. 1992. The evolution of life histories; theory and analysis. Chapman & Hall, New York, New York.

Rohner, C., and C. J. Krebs. 1998. Responses of great horned owls to experimental 'hot spots' of snowshoe hare density. Auk **115**: 694-705.

Saino, N., S. Calza, P. Ninni, and N. P. Møller. 1999. Barn swallows trade survival against offspring condition and immunocompetence. Journal of Animal Ecology **68**: 999-1009.

Sall, J., and A. Lehman. 1996. JMP® start statistics: a guide to statistical and data analysis using JMP® and JMP IN® software. Duxbury Press, Belmont, California.

Sanders, T. A. B. 1999. Essential fatty acid requirements of vegetarians in pregnancy, lactation, and infancy. American Journal of Clinical Nutrition **70 (suppl)**:: 555S-559S.

SAS Institute Inc. 1997. JMP-IN. Cary, NC.

SAS Institute Inc. 1998. Statview. Cary, NC..

Sauer, F. D., V. Fellner, R. Kinsman, J. K. G. Kramer, H. A. Jackson, A. J. Lee, and S. Chen. 1998. Methane output and lactation response in Holstein cattle with monensin or unsaturated fat added to the diet. Journal of Animal Science **76**: 906-914.

Schingoethe, D. J., M. J. Brouk, K. D. Lightfield, and R. J. Baer. 1996. Lactational responses of dairy cows fed unsaturated fat from extruded soybeans or sunflower seeds. Journal of Dairy Science **79**: 1244-9.

Schwartz, O. A., K. B. Armitage, and D. Van Vuren. 1998. A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). Journal of Zoology (London) **246**: 337-346.

Shaw, W. T. 1926. Age of the animal and slope of the ground surface, factors modifying the structure of hibernation dens of ground squirrels. Journal of Mammalogy **7**: 91-96.

Sheikina, N. V., and V. A. Serdiuk. 1978. Seasonal shifts in the chemical makeup of the fatty tissue of the Arctic suslik, Citellus parryii. Zhurnal Evol Biokhim Fiziologiia **14**: 29-33.

Simpson, M. R. 1990. Observation of an Arctic ground squirrel, *Spermophilus parryii*, - Short-tailed Weasel, *Mustela erminea*, interaction. The Canadian Field-Naturalist **104**: 473-474.

Sinclair, A. R. E. 1989. Population regulation in animals. 197-241 *in* J. M. Cherret, editor, Ecological concepts. Blackwell, Oxford,

Sinclair, A. R. E. 1996. Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. 127-154 *in* R. B. Floyd, A. W. Sheppard, and P. J. De Barro, editors, Frontiers of population ecology. CSIRO Publishing, Melbourne,

Sinclair, A. R. E., and R. P. Pech. 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos **75**: 164-173.

Skogland, T. 1983. The effects of density dependent resource limitation on size of wild reindeer. Oecologia **60**: 156-168.

Skogland, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. Journal of Animal Ecology **54**: 359-374.

Slade, N. A., and D. F. Balph. 1974. Population ecology of Uinta ground squirrels. Ecology **55**: 989-1003.

Smith, G. W., and D. R. Johnson. 1985. Demography of a Townsend ground squirrel population in southwestern Idaho. Ecology **66**: 171-178.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, New York, NY.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Strong, D. R. 1984. Density-vague ecology and liberal population regulation in insects. 313-327 *in* P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, editors, A new ecology. Wiley, New York,

Svendsen, G. E. 1976. Structure and location of burrows of yellow-bellied marmot. The Southwestern Naturalist **20**: 487-494.

Tabachnick, B. G., and L. S. Fidell. 1996. Using Multivariate Statistics. Harper Collins, New York, NY.

Thompson, T. A., M. W. Agar, and G. L. Bintz. 1993. Lipid deposition and use by black-tailed Prairie dogs, *Cynomys ludovicianus*, in the natural environment. Physiological Zoology **66**: 561-579.

Thorp, C. R., P. K. Ram, and G. L. Florant. 1994. Diet alters metabolic rate in the Yellow-bellied marmot (*Marmota flaviventris*) during hibernation. Physiological Zoology **67**: 1213-1229.

Travis, J. M. J., D. J. Murrell, and C. Dytham. 1999. The evolution of density-dependent dispersal. Proceedings of the Royal Society of London Series B **266**: 1837-1842.

Turchin, P. 1990. Rarity of density dependence or population regulation with lags? Nature **344**: 660-663.

Turchin, P. 1995. Population regulation: old arguments and a new synthesis. 19-40 *in* N. Cappuccino and P. W. Price, editors, Population dynamics: new approaches and synthesis. Academic Press, Inc., London, Turchin, P. 1999. Population regulation: a synthetic view. Oikos **84**: 153-159.

Uvarov, B. P. 1931. Insects and climate. Transactions of the Entomological Society of London **79**: 174-186.

Van Horne, B., G. S. Olson, R. L. Schooley, J. G. Corn, and K. P. Burnham. 1997. Effects of drought and prolonged winter on Townsend's ground squirrel demography in shrubsteppe habitats. Ecological Monographs **67**: 295-315.

Wauters, L. A., and L. Lens. 1995. Effects of food availability and density on red squirrel (*Sciurus vulgaris*) reproduction. Ecology **76**: 2460-2469.

Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution **11**: 398-411.

Williams, G. C. 1966a. Adaptation and natural selection. Princeton University Press, Princeton, New Jersey, USA.

Williams, G. C. 1966b. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist **100**: 687-690.

Wolda, H. 1995. The demise of the population regulation controversy? Researches on Population Ecology **37**: 91-93.

Yanez, E., D. Ivanovic, D. F. Owen, and D. Ballester. 1983. Chemical and nutritional evaluation of sweet lupines. Annals of Nutrition and Metabolism **27**: 513-20.

Yazbeck, J., M. Goubern, C. Senault, M. F. Chapey, and R. Portet. 1989. The effects of essential fatty acid deficiency on brown adipose tissue activity in rats maintained at thermal neutrality. Comparative Biochemistry and Physiology **94A**: 273-276.

Young, P. J. 1988. Ecological and energetic aspects of hibernation of Columbian ground squirrels in relation to patterns of over-winter survival. PhD Thesis. University of Alberta, Edmonton, Alberta.

Young, P. J. 1990. Structure, location and availability of hibernacula of Columbian ground squirrels (*Spermophilus columbianus*). American Midland Naturalist **123**: 357-364.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.