

**Arctic ground squirrels in the Southwest Yukon Territory:
Evidence for Habitat Specific Demography and Source-sink Dynamics**

by

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Abstract

Arctic ground squirrels (*Urocitellus parryii plesius*) of the southwest Yukon Territory occupy three distinct habitat types: boreal forest, low elevation meadows and alpine areas. Populations in boreal forest habitat have been shown to be synchronous with the 10-year snowshoe hare (*Lepus americanus*) cycle in the region due to shared predators. Relatively little is known about arctic ground squirrel populations occupying low altitude meadow and alpine meadow habitat types. Since 2000, populations in the boreal forest have remained low and in some locations have been extirpated.

The first objective of this study was to investigate the distribution and abundance of arctic ground squirrels in different habitats over a large spatial scale. Density and relative abundance data were collected at numerous locations in boreal forest, low elevation meadow and alpine meadow habitat types. Populations in the boreal forest were found to be extirpated while those in low elevation meadow habitat contained self-sustaining populations that were significantly larger. The extirpation of ground squirrels from the boreal forest and continued persistence of populations in low elevation meadow habitat suggests that the boreal forest may be functioning as sink habitat and that low elevation and alpine meadows are population sources.

The second objective of this study was to more closely investigate the population dynamics of arctic ground squirrels in boreal forest, low elevation meadow and alpine meadow habitats. Survivorship and movement data collected provide empirical evidence for the existence of source-sink dynamics between low elevation meadow (source) and boreal forest habitat (sink). The existence of source-sink dynamics between boreal forest and low-elevation meadow habitat appears to be implicated in the current prolonged low in the 10-year snowshoe hare cycle due to sustained predation pressure in the boreal forest.

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Chapter 1-Introduction

Understanding the demographic consequences of species occupying different habitats is necessary for studying how population dynamics operate over large spatial scales (Brown 1984, Krebs 1985, Kareiva et al. 1990, Pulliam 2000, Breininger et al. 2009). Wildlife populations often exist in a habitat mosaic producing variation in densities over the landscape. Changes in local population dynamics through this patchwork could determine the overall population trends. Census information within a single habitat has been used in the past as the primary metric for assessing habitat quality. However to be able to distinguish between good and poor quality habitat types, contemporary habitat selection theories emphasize the need for detailed demographic data in addition to basic abundance data (Van Horne 1983, Pulliam and Danielson 1991, Dias 1996, Diffendorfer 1998, Johnson 2004, Peery et al. 2006). In addition to density and abundance data, survivorship, reproduction and movement data are necessary to assess the population level consequences of habitat quality accurately. Two theories predict the demographic consequences of habitat selection, the Ideal Free Distribution (IDF) theory (Fretwell 1972) and the more recently developed Source-sink theory (Pulliam 1988).

The IDF model first described by Fretwell and Lucas (1969) describes a situation whereby the fitness of populations occupying different habitat types should eventually equalize thereby compensating for the existence of habitat specific variation in demographic rates. More recently McPeck and Holt (1992) and Ragnhild et al. (2009) propose that if an individual can actively select its habitat, there is no reason why a species should remain in a habitat type where its average fitness over time is compromised. The movement of a species that actively selects a habitat, moving from an unsuitable area to a suitable one, results in the average fitness in different habitats becoming equal. Under the IDF model a situation prevails where habitats of

varying carrying capacity exist over the landscape rather than the presence of habitat specific demographic rates.

Source-sink theory, originally described by Holt (1985) but formalized by Pulliam (1988), on the other hand describes a situation where habitat specific demographic rates can exist indefinitely. In Source-sink theory, a species occupies at least two different habitat types where a disparity in demographic rates exists. More specifically, a species occupies source habitat types and sink habitat types. Source habitat types exist where births outnumber deaths allowing for a surplus of dispersers. Conversely, in sink habitat types, deaths outnumber births and persistence would not be possible without immigration from nearby source habitats. Accurately indentifying the presence of source-sink dynamics in wildlife populations necessitates detailed demographic information (Dias 1996, Diffendorfer 1998, Peery et al. 2006, Perlut et al. 2008). Data on survivorship, reproduction and movements of a species in different habitat types, ideally over long-term periods are necessary to accommodate the inherent temporal variation in wildlife population dynamics. The concept of meta-population dynamics, first described by (Levins 1969), also describes a similar situation where conspecifics occupy spatially segregated habitat patches that are connected through dispersal; however in Levins' model, each patch has an equal likelihood of going extinct in response to stochastic processes.

Although the IDF and the Source-sink theories predict significantly different demographic outcomes for species occupying a variety of habitat types, similarities do exist between the two models. For example, both theories assume density dependent population regulation and dispersal from non-sink habitat types (Diffendorfer 1998). Major differences arise around the subject of dispersal. IDF theory predicts no net flow of movement between habitat types whereas Source-sink theory predicts a net flow of dispersers from source habitat types to

sinks (Diffendorfer 1998). Both theories have been important in guiding our understanding of spatial and temporal variation in demographic rates and evidence consistent with both theories can be found in the recent literature.

In this thesis I studied arctic ground squirrels (*Urocitellus parryii plesius*) in the Kluane Region, Yukon Territory and present data to determine how abundance and demography vary spatially and temporally. Since arctic ground squirrels occupy a range of habitat types in the Kluane Region, this species is a suitable candidate for investigating abundance in a range of habitat types and more importantly the landscape level consequences of habitat specific demographic rates.

Study Area

Arctic ground squirrels were studied in three distinct habitat types (boreal forest, low elevation meadows and alpine meadows) in the Kluane Region of the Yukon Territory, Canada. Detailed abundance and demographic data were collected at five locations. In the boreal forest, data were collected at two 10 ha study sites (~900 m asl [above seal level]) (N 61° 00' 38'' W 138° 11' 31'' and N 60° 55' 53'' W 137° 58' 25'') located ~20 km from each other (see Gillis et al. (2005) . Both boreal forest grids were dominated by white spruce forest and willow thickets with occasional aspen stands. In low elevation meadow habitat, data were collected in Kluane National Park and Reserve (KNPR). The 10 ha study site (~800 m asl) was located in the Slims river valley in south facing meadow habitat surrounded by boreal forest and by the Slims river delta immediately to the east (N 60° 59' 56'' W 138° 33' 31''). In Alpine meadow habitat, data were collected at two locations. The first 10 ha alpine meadow study site (~1600 m asl) was located in KNPR and ~8 km uphill from the low elevation meadow site in south facing alpine meadow habitat (N 61° 01' 06'' W 138° 37' 34''). The second 12 ha alpine meadow study site

(~1800 m asl)(N 61°10'57'' W 138°26'02'') was located ~30 km from the first alpine meadow study site and consisted of open, south facing meadow habitat with bare ground and boulder fields (Gillis et al. 2005).

Study Species

Arctic ground squirrels are a medium-sized burrowing rodent. Throughout the majority of their range arctic ground squirrels occupy arctic and alpine tundra habitats in Canada, Alaska and Siberia (Nadler et al. 1974, Nadler 1977). At the more southern extent of their range however arctic ground squirrels occupy a variety of habitats in addition to alpine meadows, including low elevation meadows and the boreal forest (Lacey et al. 1997, Karels et al. 2000, Boonstra et al. 2001, Krebs et al. 2001, Gillis et al. 2005).

Arctic ground squirrels spend the majority of their time in hibernation (~8-9 months) with males emerging first in mid to late April followed closely by females (McLean and Towns 1981, Lacey et al. 1997, Buck and Barnes 1999a). Females are sexually receptive ~ 1 week after emergence (Lacey et al. 1997). Young are born after a ~25 day gestation period but remain in the natal den until mid-late June and litter sizes range from 4-7 (Lacey et al. 1997). Juvenile dispersal occurs in early-mid July and is highly male biased (Lacey 1991, Byrom and Krebs 1999). Hibernation begins in late July and is initiated by adult females, followed by juvenile females, adult males and finally juvenile males (Green 1977, McLean and Towns 1981). Males can remain active until mid-late October in some instances (Green 1977).

Arctic ground squirrels have been studied extensively in the boreal forest in the Kluane region since 1990 (see (Boutin et al. 1995, Hubbs and Boonstra 1997, Byrom and Krebs 1999, Karels and Boonstra 1999, Karels et al. 2000, Hik et al. 2001, Gillis et al. 2005)) and have been shown to fluctuate with the 10-year snowshoe hare cycle in response to shared predators. Since

2000, arctic ground squirrel populations in the boreal forest have remained low and in some locations have been extirpated (Henry et al. 2007). By contrast, population sizes in alpine meadows are larger and more stable than those in the boreal forest and appear to be limited by overwintering conditions rather than by predation (Green 1977, Gillis et al. 2005). Apart from Green (1977), little information exists for arctic ground squirrel populations in low elevation meadow habitats.

Arctic ground squirrels in the Kluane region are also culturally significant. First Nation groups in the region have used arctic ground squirrels as a food and fur source for hundreds of years and continue this tradition to the present. The discovery of “Long Ago Person Found” in the Kluane region illustrates the importance of arctic ground squirrels in First Nation culture. The 500-550 year old body discovered at the foot of a glacier in the region was clothed in arctic ground squirrel pelts (Dickson et al. 2004). The disappearance of arctic ground squirrels from traditional hunting areas since 2000 has resulted in concern within local First Nation communities. Traditional capture techniques involved an eagle feather snare placed at the entrance of the burrow but more modern techniques involve the use of metal traps.

Thesis Overview

In chapter 2 I investigate the patterns of distribution and abundance of arctic ground squirrels at a number of locations in low meadow, boreal forest and alpine meadow habitats in the Kluane region. I investigate the prediction that although arctic ground squirrel populations in the boreal forest are low due to the increased predation pressure associated with the current low phase of the snowshoe hare cycle, that in nearby low meadow and alpine meadow habitat, arctic ground squirrels will be relatively abundant. Although there is evidence that populations are

smaller at low elevations, there are currently no data to determine if this pattern of low density at low elevation occurs at a larger spatial scale.

In chapter 3 I investigate the population dynamics of arctic ground squirrels in each distinct habitat type: boreal forest, low elevation meadow and alpine meadow. More specifically I predict that arctic ground squirrels display habitat specific demographic rates in the Kluane region and test the hypotheses that (1) High elevation alpine meadow habitats are population sources that provide individuals to low elevation population sinks or alternatively that (2) Low elevation habitats are characterized by two distinct habitat units, low elevation meadow (source) and boreal forest (sink) that display discrete demographic conditions independent of those at higher elevations.

Chapter 2-Habitat Specific Distribution and Abundance of Arctic Ground Squirrels (*Urocitellus parryii plesius*) in the Southwestern Yukon Territory.

Chapter Overview

Wildlife populations often occupy a variety of habitat types, particularly when studied over large spatial scales and basic con-specific abundance and distribution data in different habitat types is necessary for scientists and wildlife managers to make informed decisions regarding the status and viability of wildlife populations at regional scales. Both the Ideal Free Distribution (IDF) and Source-Sink theories have been developed to explain the spatial distribution of wildlife populations in different habitat types. Here I study Arctic ground squirrels (*Urocitellus parryii plesius*) in the Kluane region of the Southwest Yukon Territory, Canada that occupy three distinct habitat types; boreal forest, low altitude meadows and alpine meadows to determine if populations in these different habitats provide evidence for IDF or source-sink theory. Most studies have focused on arctic ground squirrel populations in boreal forest habitat and have concluded that abundance is synchronous with the 10-year snowshoe hare (*Lepus americanus*) cycle in the region due to shared predators. Relatively little is known about arctic ground squirrel populations occupying low altitude meadow and alpine meadow habitat types. Here I assess the current distribution and abundance of arctic ground squirrels in these three habitat types and predict that although populations in the boreal forest are likely low due to increased predation pressures associated with the current low phase of the snowshoe hare cycle, that in nearby low altitude meadow and alpine meadow habitat, ground squirrels will be relatively abundant.

Average late summer densities differed significantly among habitat types with $0.38 \pm 0.13(1 \text{ SE})/\text{ha}$ in boreal forest habitat, $1.25 \pm 0.22/\text{ha}$ in low altitude meadow habitat and 5.7

$\pm 0.22/\text{ha}$ in alpine meadow habitat. From 2008-2010 when densities measurements were concurrent, ground squirrels had been extirpated from boreal forest habitat, while densities in low meadow and alpine meadow habitat were $1.6 \pm 0.34/\text{ha}$ and $6.1 \pm 0.7/\text{ha}$ respectively. I also found major differences in arctic ground squirrel relative abundance in these three habitat types with 0.1 ± 6.2 active burrows/ha in the boreal forest, 64.0 ± 5.3 active burrows/ha in low elevation meadows and 332.3 ± 85 active burrows/ha in alpine meadows. The total number of burrows/ha (active plus inactive) however did not differ between boreal forest and low meadow habitat (196 ± 9 and 225 ± 9 total burrows/ha respectively). Alpine meadow habitat contained a considerably higher density of burrows (681 ± 8 total burrows/ha).

In accordance with my prediction, arctic ground squirrel population size in the boreal forest remained low compared with populations in nearby low elevation meadow and alpine meadow habitat. The low densities and abundance of arctic ground squirrels in the boreal forest is likely due to the recent prolonged low phase of the snowshoe hare cycle because of sustained predation pressure in this habitat type. The recent extirpation of ground squirrels from the boreal forest and the persistence of populations in low meadow and alpine meadow habitat suggest that the boreal forest is sink habitat and that low and high elevation meadows are population sources.

Introduction

Understanding the demographic implications of conspecifics occupying different habitats is necessary for studying how population dynamics operate over large spatial scales and is of fundamental importance in the field of ecology (Brown 1984, Krebs 1985, Kareiva et al. 1990, Pulliam 2000, Breininger et al. 2009). Wildlife populations often exist in a habitat mosaic producing variation in densities over the landscape and changes in local population dynamics through this patchwork can determine the overall population trends.

Two theories predict the demographic consequences of habitat selection, the Ideal Free Distribution (IDF) theory (Fretwell 1972) and Source-sink theory (Pulliam 1988). The IDF model first described by Fretwell and Lucas (1969) describes a situation whereby the fitness of populations occupying different habitat types should eventually equalize thereby compensating for the existence of habitat specific variation in demographic rates. More recently McPeck and Holt (1992b) and later Ragnhild et al. (2009) propose that if an individual can actively select its habitat, there is no reason why a species should remain in a habitat type where its average fitness over time is compromised. In the IDF model a situation prevails where habitats of varying carrying capacity exist over the landscape rather than the presence of habitat specific demographic rates.

Source-sink theory, originally described by Holt (1985) but formalized by Pulliam (1988) on the other hand describes a situation where habitat specific demographic rates can exist indefinitely. In Source-sink theory, a species occupies at least two different habitat types where a disparity in demographic rates exists. More specifically, a species occupies source habitat types and sink habitat types. Source habitat types exist where births outnumber deaths allowing for a surplus of dispersers. Conversely, in sink habitat types, deaths outnumber births and persistence would not be possible without immigration from nearby source habitats. Source-sink theory developed from the concept of meta-population dynamics first described by Levins (1969). Meta-population theory describes a similar situation where conspecifics occupy spatially segregated habitat patches that are connected through dispersal. However in Levins' model, each patch has an equal likelihood of going extinct in response to stochastic processes. In Source-sink theory, only sink habitats should experience extinction events.

Both theories have been important in guiding our understanding of spatial and temporal variation in demographic rates and evidence consistent with both theories can be found in the recent literature. Nystrand et al. (2009) studying Siberian jays (*Perisoreus infaustus*) showed how the regional population dynamics of a species can vary tremendously depending on the habitat type occupied. Similarly, Kreuzer and Huntly (2003) studying American pika (*Ochotona princeps*) populations in different habitats found evidence for habitat specific demographic rates and the presence of a source-sink dynamic (Pulliam 1988). A single species that occupies a variety of habitat types therefore necessitates detailed investigation in all habitats in order to make accurate conclusions about large scale population dynamics.

Arctic ground squirrels provide the opportunity to investigate the potential for habitat specific demographic rates and provide support for IDF or Source-sink theory. Arctic ground squirrels occupy a large geographic range mostly occupied by arctic tundra and alpine areas in North America and Siberia (Nadler 1977). Arctic ground squirrel populations in arctic tundra and alpine environments support high densities, remain stable and appear to be limited by predation and burrow availability (Carl 1971, Green 1977, Buck and Barnes 1999a). In the southern part of their range however, arctic ground squirrels occupy a variety of habitat types including boreal forest, low altitude meadows and alpine meadows (Green 1977, Lacey 1991, Krebs et al. 2001, Gillis et al. 2005). The majority of studies have focused on the population ecology of arctic ground squirrel populations in boreal forest habitat (Byrom et al. 2000, Karels et al. 2000, Krebs et al. 2001), but see Gillis et al. (2005) and Green (1977). Boutin et al. (1995) have shown that arctic ground squirrel populations in the boreal forest of the southwest Yukon exhibit synchronous fluctuations with the 10-year snowshoe hare (*Lepus americanus*) cycle likely due to shared predators. Arctic ground squirrel populations in the boreal forest have been studied in the

southwest Yukon since 1990 with densities ranging from 3.3/ha during the snowshoe hare peak to 0.4/ha during the snowshoe hare low phase (Boutin et al. 1995, Gillis et al. 2005). Since the majority of studies in the Kluane Region have focused on ground squirrels in the boreal forest, relatively little is known about ground squirrel populations occupying both low elevation meadow and alpine meadow habitat types.

Here I assess the current distribution and abundance of arctic ground squirrels by measuring density and indexing populations in three different habitat types. I measured population density by extensive live trapping in low meadow and alpine meadow habitat from 2008-2010. Density data were also compiled from Green (1977) studying arctic ground squirrels in the same low meadow and alpine meadow sites that I used for this study. I compared these density data to data from Krebs et al. (2009) who studied arctic ground squirrels in boreal forest habitat. I also used a powder tracking technique to assess arctic ground squirrel relative abundance in boreal forest, low meadow and alpine meadow habitats in other areas of the Kluane region. I predict that although density in the boreal forest is likely low due to intense predation pressure associated with the current low densities of the snowshoe hare (Sheriff et al. 2009), whereas in nearby low and alpine meadow habitats arctic ground squirrel populations are relatively abundant.

Methods

Study Species Arctic ground squirrels occupy arctic tundra, alpine areas and the boreal forest of Canada and Alaska (Nadler 1977). The majority of arctic ground squirrel life history is occupied by a 8-9 month period of hibernation from late July/early August to late April/early May (Carl 1971, Lacey 1991). Females breed almost immediately upon emergence in spring and produce one litter per year approximately 25 days later in mid-May (Green 1977, Lacey 1991,

Lacey et al. 1997). Juveniles emerge from the natal burrow in mid to late June and begin to disperse by mid-July. Juvenile arctic ground squirrel dispersal has been shown to be highly male biased (Byrom and Krebs 1999).

Study Area Arctic ground squirrels were studied in three distinct habitat types (low elevation meadow, boreal forest, and alpine meadow) in the Kluane Region of the Yukon Territory, Canada (Figure 1). Detailed density data were collected at four locations. In the boreal forest, data were collected at two 10 ha study sites (~900 m (asl)[above sea level]) (N 61° 00' 38'' W 138° 11' 31'' and N 60° 55' 53'' W 137° 58' 25'') located ~20 km from each other (see Gillis et al. 2005). Both boreal forest grids were dominated by white spruce forest and willow thickets with occasional aspen stands. In low elevation meadow habitat, data were collected in Kluane National Park and Reserve (KNPR). The 10 ha study site (~800 m asl) was located in the Slims River valley in south facing meadow habitat surrounded by boreal forest and by the Slims River delta immediately to the east (N 60° 59' 56'' W 138° 33' 31''). In Alpine meadow habitat, data were collected at one location. The alpine meadow study site (~1600 m asl) was located in KNPR and ~8 km uphill from the low elevation meadow site in south facing alpine meadow habitat (N 61° 01' 06'' W 138° 37' 34''). Data for the boreal forest were compiled from Krebs et al. (2001), Gillis et al. (2005) and Krebs et al. (2009). Additional data for low elevation meadow and alpine meadow habitat were compiled from Green (1977).

Trapping and Handling This research was approved by the University of British Columbia Animal Care Committee in accordance with the guidelines of the Canadian Council for Animal Care. In the boreal forest, arctic ground squirrels were live trapped on a 10 ha grid with traps spaced 30 m apart in a 10x10 array with traps placed at alternate grid stakes. At the low elevation meadow site, squirrels were trapped on a 9 ha grid with traps spaced 50 m apart in a 5x10 array

at each grid stake. At the alpine meadow site in KNPR, trapping occurred on a 9 ha grid with traps placed 50 m apart in a 7x7 array with traps at each grid stake. Squirrels were trapped using Tomahawk live traps (14 x 14 x 40 cm, Tomahawk live trap Co., Tomahawk, Wisconsin) baited with peanut butter. Upon capture squirrels were transferred to a mesh bag, tagged with monel No. 1005-1 tags (National Band and Tag Co., Newport, Kentucky) in both ears (first capture only), weighed with a Pesola spring scale (± 5 g), sexed and measurements of skull width (± 0.5 mm) were taken.

Density Population density data for all habitat types were obtained by mark-recapture methods. Each mark-recapture session consisted of 2-6 consecutive days of trapping in late July early-August. Traps were set at 0800 h at each permanent trapping location, checked every 1.5 hours and closed by 1230 h each trapping day. All density estimates were calculated using the maximum likelihood (ML) spatial model within program Density 4.4 (Efford 2007, Efford et al. 2009). The ML spatially explicit capture-recapture model in program Density 4.4 was used since this model seems to provide the most accurate density estimates for small mammals (Krebs et al. 2010).

Relative Abundance We indexed 18 ground squirrel populations throughout a 400,000 ha area in the Kluane Region. Populations were indexed in boreal forest, low elevation meadow and alpine meadow to determine how arctic ground squirrels are currently distributed in these different habitat types. We used a powder tracking methodology described by Hubbs et al. (2000). The 5x7 cm tiles were placed in all known burrows in a specified area and left for 6-hours. The tiles were covered lightly in paraffin based oil and talcum powder. We retrieved the tiles and determined whether the burrow was active or inactive. If the tile was moved or covered in soil or tracks, the burrow was considered active. The area of each site indexed was determined

by recording the GPS coordinates of the corners of the site and then using the computer program MapSource (Garmin Corporation, 2004) to estimate the area in hectares. The area was used to calculate an estimate of active burrows/ha and total burrows/ha. In the event of a discrepancy between the number of tiles deployed and the number of tiles retrieved, the number of tiles deployed was used in the burrow density calculation and the number of tiles retrieved was used to determine active burrows density. To minimize bias associated with juvenile emergence in mid June and variation between sites, all locations were indexed between mid-May and mid-June. Since arctic ground squirrel activity is influenced by both time of day and weather, all indexing was carried out between 0800 h and 1600 h each day and during clear weather conditions.

Statistical Analyses All data are given as means \pm SE. All statistical analyses were calculated using program JMP v4.0 (SAS institute, Cary, NC). Averaged arctic ground squirrel densities, burrows/ha and active burrows/ha were analyzed using a one-way ANOVA with Tukey's post-hoc tests. Prior to analysis all data were assessed for normality and homogeneity of variance. Both density and relative abundance data did not meet the assumptions of normality and were transformed. A log transformation was applied to the density data and relative abundance data were square root transformed to meet the assumptions of normality and equal variance.

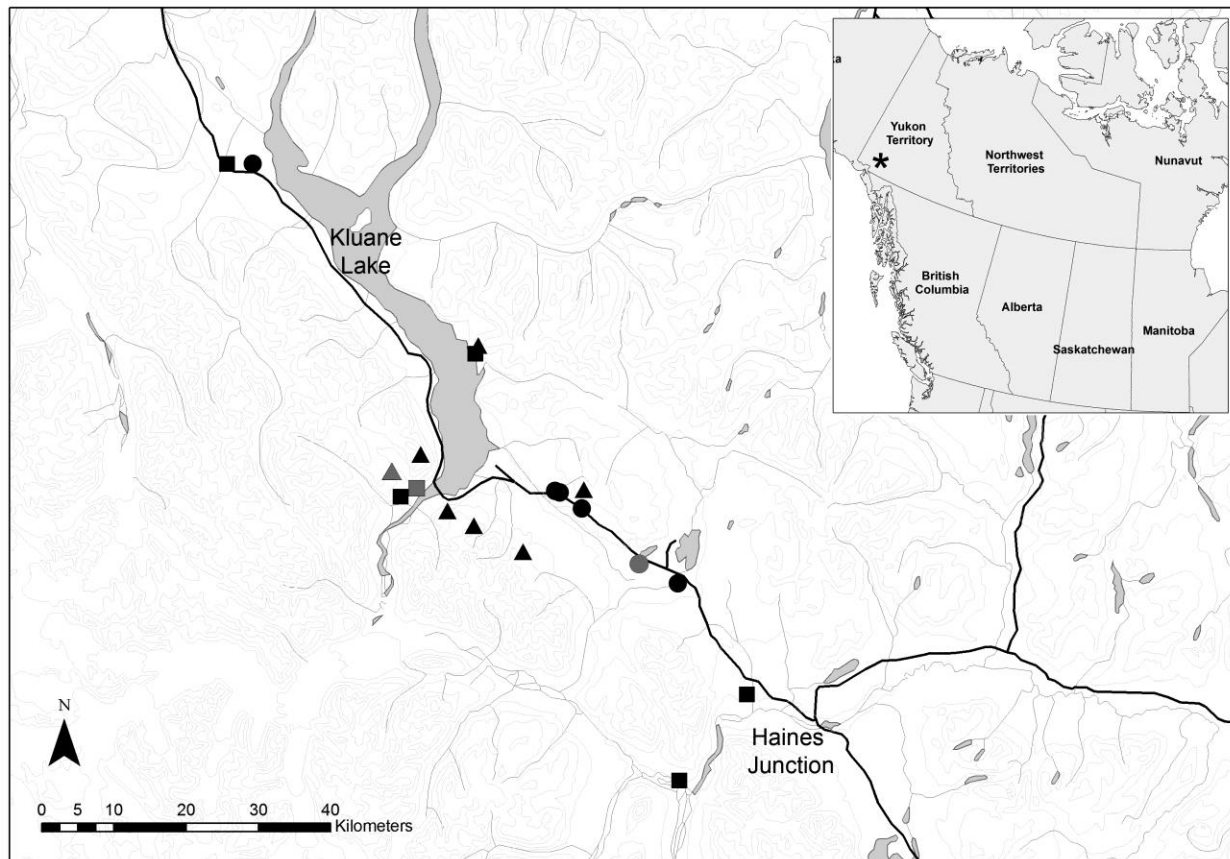


Figure 1 Study Area location. Dark circles represent boreal forest study areas, dark squares represent low meadow study areas and dark triangles represent alpine meadow study areas. Light grey shading represents areas where both density and relative abundance measures were taken.

Results

Density Yearly late summer densities along with concurrent snowshoe hare densities are displayed in Figure 2. Average late summer densities differed significantly between all habitat types. ($F_{2,19}$, $P > 0.0001$) (Figure 3). Densities were lowest in the boreal forest ($0.38 \pm 0.13/\text{ha}$) higher in low meadow ($1.25 \pm 0.22/\text{ha}$) and highest in alpine meadow habitat ($5.7 \pm 0.22/\text{ha}$). This pattern is evident in both the long term density data and in data from the more recent extensive trapping in all three habitat types during 2008 and 2009. Densities in the boreal forest did not recover following the recent snowshoe hare peak in 2006. These populations have been extirpated from this habitat type. However densities in nearby low meadow habitat remained stable during this same time period. Densities were $1.4 \pm 0.3/\text{ha}$ in 2008 and $1.6 \pm 0.34/\text{ha}$ in 2009. Densities monitored in alpine meadow habitat were $5.0 \pm 0.57/\text{ha}$ in 2008 and $6.1 \pm 0.7/\text{ha}$ in 2009.

Relative Abundance A total of 18 populations were indexed throughout the Kluane region (5 boreal forest habitats, 6 low elevation meadow habitats, 7 alpine meadow habitats) I found that the regional densities showed a similar pattern to our intensively live trapped areas (shown above). The number of active burrows/ha increased from 0.1 ± 5.3 in the boreal forest to 64.0 ± 5.3 in low elevation meadows to 332.3 ± 85.0 in alpine meadows ($F_{2,17}$, $P < 0.0001$; Figure 4). The total number of burrows/ha however did not differ between boreal forest (196 ± 9.0) and low meadow habitat (225 ± 9.0), but alpine meadow habitat contained a considerably higher density of burrows (681 ± 8.0) ($F_{2,17}$, $P < 0.01$) (Figure 4).

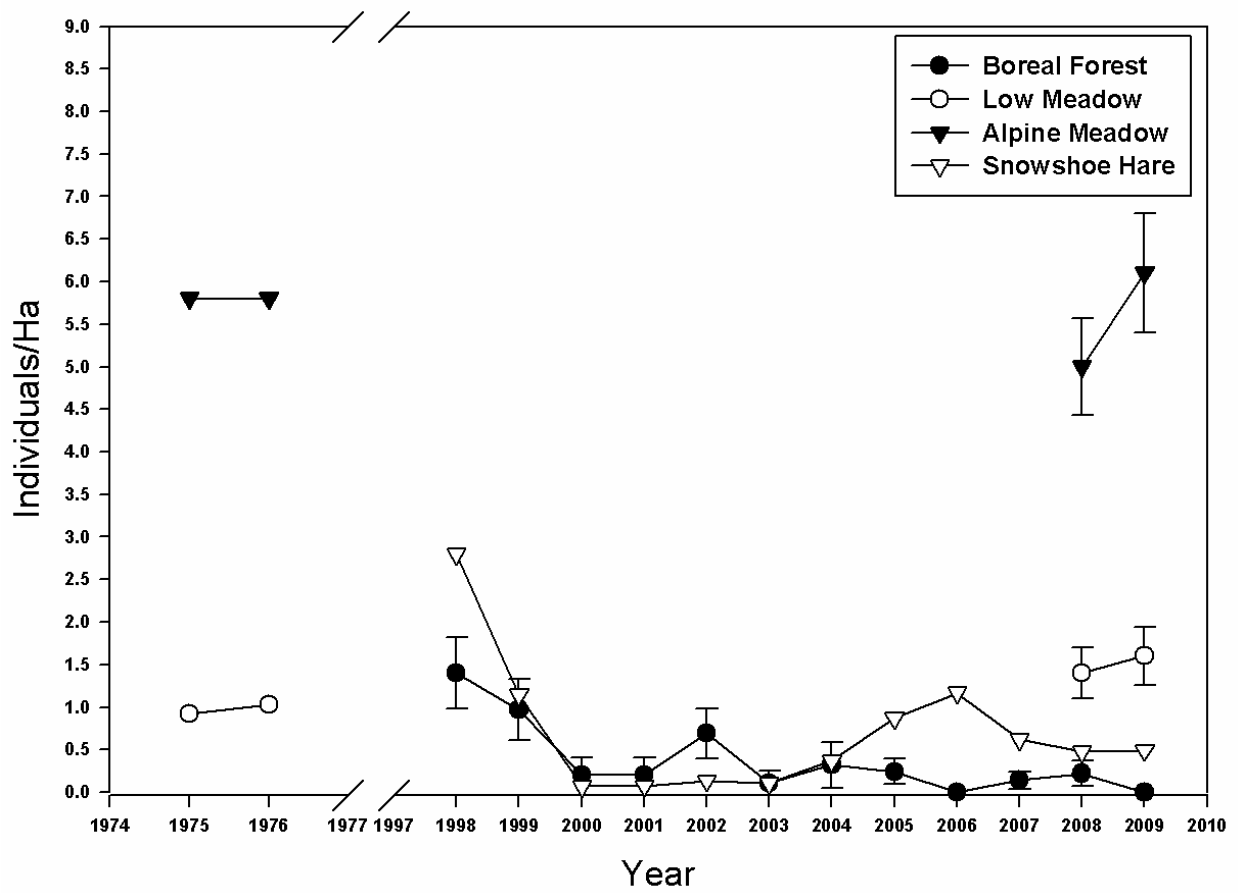


Figure 2 Density estimates of arctic ground squirrels in three different habitat types in the Kluane region, Yukon Territory. Bars represent 1 SE.(source: 1975-1976 data (Green 1977), boreal data (Krebs et al. 2009, unpubl.). Snowshoe hare densities from Krebs et al. 2009, unpubl..

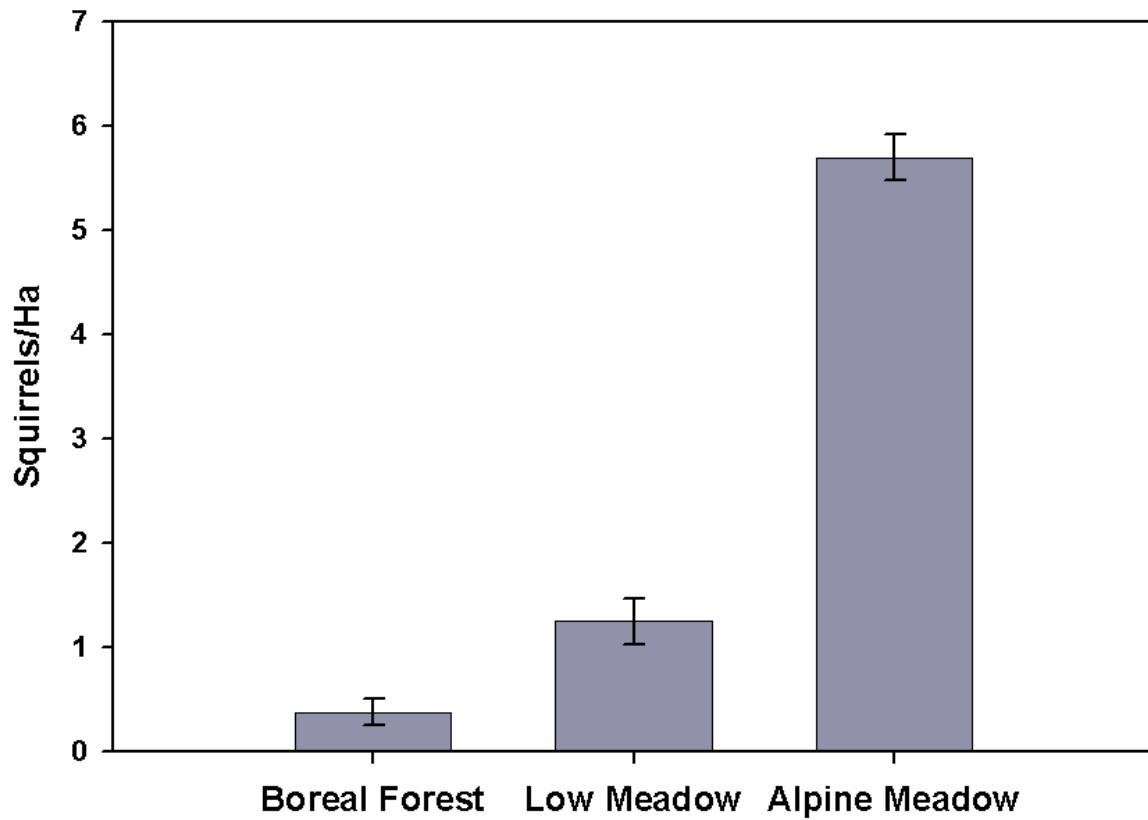


Figure 3 Average densities of arctic ground squirrels in the Kluane region, Yukon Territory. Bars represent means \pm 1 SE. boreal forest n=12 (1998-2009), low meadow n=4 (1975,1976, 2008,2009), alpine meadow n=4(1975,1976,2008,2009)(source:1975-1976 Green (1977), boreal forest Krebs et al. (2009,unpubl.)).

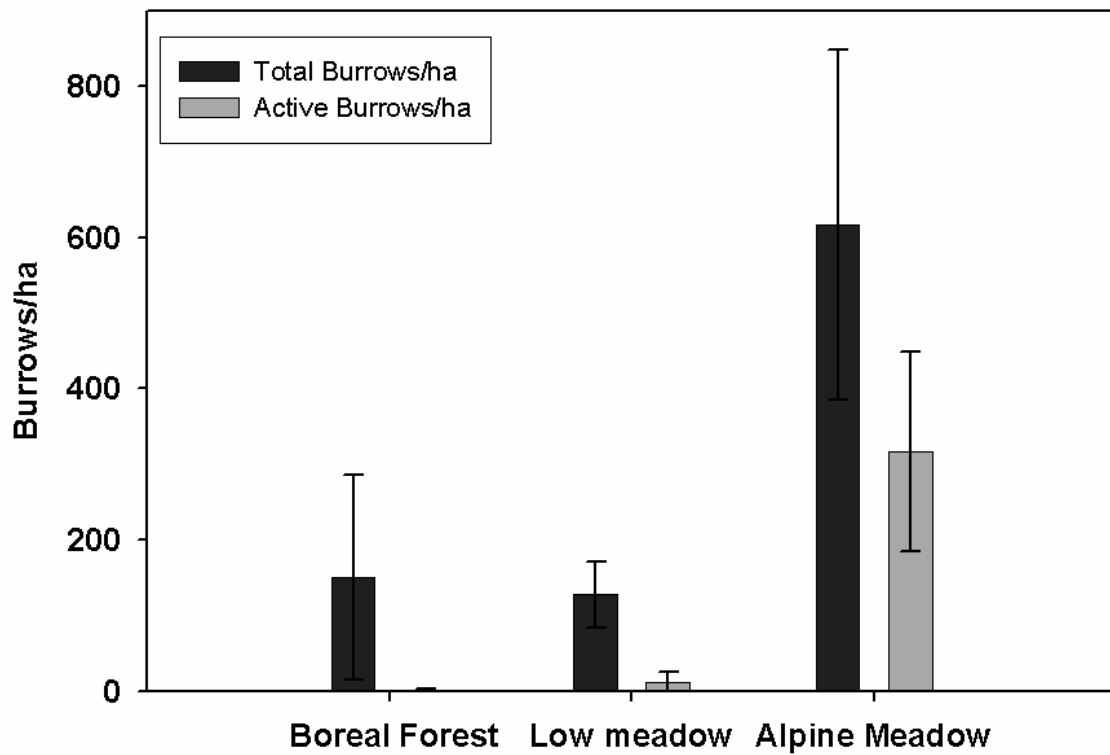


Figure 4 Relative abundance of arctic ground squirrels in different habitat types from 2008-2010 in the Kluane region, Yukon Territory. Bars represent 1 SE. boreal forest n=5, low meadow n=6, alpine meadow n=7.

Discussion

Both the density data and the regional population index data I collected in this study show that arctic ground squirrel density and relative abundance was lowest in the boreal forest, higher in nearby low meadows and highest in alpine meadows. In 2006, ground squirrel populations in the boreal forest were extirpated. This habitat was subsequently re-colonized by 3 individuals in 2007. This population went extinct again in 2009 (Figure 2). In contrast, densities measured concurrently in nearby low meadow and alpine meadow habitat in 2008 and 2009 were significantly greater than those in the boreal forest and were very similar to those reported by Green (1977) (Figure 2), also studying arctic ground squirrels during the low phase of the snowshoe hare cycle. The regional abundance data (Figure 4) also displayed a similar pattern to that of measured density with ground squirrel relative abundance increasing significantly from boreal forest to low meadow to alpine meadow habitat.

The ecological factors driving these density differences among habitats include predation, food limitation, burrow limitation, disease, and climatic changes. Top-down limitation is likely an important factor continuing to limit ground squirrel populations in the boreal forest. For example, in the boreal forest populations typically exhibit cyclical fluctuations that are positively correlated with the 8-10 year snowshoe hare cycle, but with a lag of 1-2 years (Boutin et al. 1995, Krebs et al. 2001). This lag is likely due to prey switching (Hubbs and Boonstra 1997). The increase phase of the hare cycle likely relieves predation pressure on arctic ground squirrels, a secondary prey species in the boreal forest, given the increasing abundance of the primary prey species in this habitat type, the snowshoe hare. Ground squirrel population sizes in the boreal forest started to decline in 1998 likely in response to the concurrent decline in snowshoe hare abundance and ground squirrels have remained low from 1998 to the present. Snowshoe hare densities in the boreal forest began to increase again in 2004 with peak densities occurring in

2006, however these most recent peak was less than half of those observed during the previous peak in 1998 (0.92 hares/ha in the 2006 peak vs. 1.98 hares/ha in 1998 (Sheriff et al. 2009).

Numerous studies on arctic ground squirrels in the boreal forest have found predation to be a major limiting factor particularly during times when snowshoe hare densities are low (Hubbs and Boonstra 1997, Karels and Boonstra 1999, Byrom et al. 2000, Karels et al. 2000, Gillis et al. 2005). The failure of populations to recover in the boreal forest is likely implicated in the recent sustained low phase of the snowshoe hare cycle. Studies comparing survival rates in boreal forest, low meadow and alpine meadow habitats will help elucidate the importance of predation in limiting boreal forest arctic ground squirrel populations.

Although the importance of food limitation in regulating herbivore populations has been disputed, it is possible that interactions between resource limitation and predation are inhibiting the recovery of boreal populations. For example in food addition and predator exclusion experiments, arctic ground squirrel densities increased to 19 times those observed on control plots (Karels et al. 2000). It is unlikely that food availability in boreal forest habitat has changed since 1998 when populations started to decline however this needs to be explored further empirically by examining growth rates and body condition in different habitat types (see appendix A).

The similar number of burrows in boreal forest and low altitude meadow habitat (196 ± 9.0 and 225 ± 9.0 respectively) suggests that the availability of burrows is not a limiting factor for arctic ground squirrels in the boreal forest. The observed density differences between boreal forest, low meadow and alpine meadow habitats and the negligible difference in the total number of burrows/ha between the boreal forest and low meadow suggests that burrow availability is similar and that another process is driving the observed density differences. Although burrow

limitation can be a significant limiting factor for populations in alpine and arctic tundra (Carl 1971, Batzli and Sobaski 1980), the majority of studies investigating boreal and sub-boreal ground squirrel populations have not found burrow limitation to be a major limiting factor (Karels et al. 2000, Sherman and Runge 2002, Greene et al. 2009).

Another potential limiting factor in the boreal forest is disease. During live-trapping of arctic ground squirrels in previous studies in the Kluane region there were no indications of disease found in boreal forest populations. Also, given the close proximity of boreal forest populations to those in nearby low meadow habitats, a disease present in the boreal forest would likely manifest itself in these low meadow populations, something that was not observed during this study. Although there is some evidence for the ability of disease to limit ground squirrel populations (see (Smith and Johnson 1985, Cully et al. 2001)), there has been no indication of the presence of disease or disease outbreaks in arctic ground squirrel populations in the boreal forest. Climatic changes are expected to be the most pronounced in the Polar Regions and these changes may have the capacity to alter arctic ground squirrel population dynamics both directly and indirectly. Direct effects include the increasing occurrence of winter rain events. Winter rain events may affect hibernating ground squirrels in two important ways; reducing snowpack and by directly flooding burrows. Winter rain events in the Kluane region have increased in occurrence since 2000 (Environment Canada Canadian Climate Normals). Although significant rain events occurred in winters between 2000 to 2007, there were no major winter rain events observed during the course of this study from 2008 to 2010. Since arctic ground squirrels produce yearly litter sizes ranging from 2-6, the time frame of this study should have allowed for populations in the boreal forest to recover if winter rain was a limiting factor. Winter rain should

have also affected populations in nearby low meadows but the results from this study suggest populations have remained stable in this habitat type.

Indirect effects of climatic change on boreal populations include the potential effects that climatic changes impose on the snowshoe hare cycle. Since populations in the boreal forest have historically been correlated with changes in the 9-10 year snowshoe hare cycle, changes in this cycle will presumably have important consequences for arctic ground squirrels in the boreal forest. Although the factors responsible for explaining the recent prolonged low phase of the snowshoe hare cycle continue to be investigated (Sheriff et al. 2009), relating climatic variability to variability in wildlife population dynamics remains challenging (Krebs and Berteaux 2006). A detailed demographic study in concert with long-term monitoring data in different habitat types will also help clarify the potential impacts of climate change on arctic ground squirrel population dynamics.

Conclusion

The persistence of arctic ground squirrels in low and high elevation meadow habitat and the concurrent extinction of arctic ground squirrels from areas in the boreal forest provide evidence for the existence of source-sink dynamics. It appears that the boreal forest habitat is functioning as a population sink that relies on immigration from nearby meadow habitat to persist, although this needs to be explored further empirically. While density data alone are often insufficient to assess habitat quality, abundance data collected concurrently over large spatial scales and in different habitat types can be useful for both scientists and managers to initiate further, more detailed investigations. This information can be used to make broader ecological inferences and formulate more specific hypotheses about what factors are driving the population dynamics of wildlife populations occupying heterogeneous habitat types. Here I show that arctic

ground squirrel density and abundance varies considerably depending on habitat type. These findings illustrate the importance of being cautious when interpreting data collected in a single habitat type and using this data to infer the status of a wildlife population over larger spatial scales. For example, conclusions about the status of ground squirrels in the Southwest Yukon based on data collected in boreal forest habitat would be inaccurate in the absence of data collected in low meadow or alpine meadow habitats. It is apparent that the mechanisms underlying the large variation in density in boreal forest, low meadow and alpine meadow habitats need to be further explored empirically and future research should focus on the demographic processes responsible for these habitat differences.

Chapter 3-Evidence for Source-Sink Dynamics in the Arctic Ground Squirrel (*Urocitellus parryii plesius*)

Chapter Overview

Wildlife populations with large geographic ranges often occupy a variety of different habitat types and may exhibit variable demographic rates. Variable demographic rates can manifest themselves between habitat types in the form of source-sink dynamics where populations in sink habitats would not exist without the addition of migrants from source habitats. The presence of source-sink population dynamics has important implications for scientists and managers since the temporal absence of a species from sink habitat may be expected and not indicative of the status of the wildlife population at larger spatial scales. Alternatively, trends detected in source habitats will likely be more indicative of real changes within a wildlife population and justify management concern. Although source-sink population dynamics are theoretically understood, there is a paucity of empirical evidence for their existence in wildlife populations.

Arctic ground squirrels (*Urocitellus parryii plesius*) occupy a large geographic area in northern Canada and a variety of habitat types within this area including boreal forest, low altitude meadows and alpine meadows. Since 2000, populations of arctic ground squirrels in boreal forest habitat in the southwestern Yukon have remained low and in some instances become extirpated, whereas those in nearby low altitude meadows and alpine meadows have remained stable suggesting that this species may exhibit source-sink population dynamics. In this study I tested the hypothesis that arctic ground squirrels exhibit source-sink population structure and more specifically that alpine meadow populations function as population sources for both low altitude meadows and boreal forest habitat. The alternative hypothesis is that low elevation

habitats are demographically separate from higher altitude alpine habitats and consist of low altitude meadow habitats (sources) and boreal forest habitat (sinks).

My evidence rejects the first hypothesis and supports the alternative. Active season survival in the boreal forest was significantly lower than in low altitude meadow and alpine meadow habitat (43% vs. 73% and 80% respectively). Overwinter survival was similar among the three habitat types (65%, 66% and 51% respectively). Radio-collared juveniles born in low altitude meadow habitat moved significantly further than collared individuals in alpine meadow habitat (319m vs. 76m). Of the radio collared juveniles in low altitude meadow habitat, 65% (n=11) moved into boreal forest habitat and of these, 73% (n=8) were subsequently predated. Conversely, 100% (n=6) of radio collared individuals that remained in low altitude meadow habitat survived the 38-day tracking period. Boreal forest habitat also exhibited a significantly lower recruitment rate (juveniles per adult) compared with both low altitude meadow and high elevation alpine meadow habitat (0.44, 1.14 and 1.41 respectively). Rates of population growth (λ) values calculated in program MARK were 0.68, 0.90 and 0.98 respectively for boreal forest, low altitude meadow and alpine meadow habitat.

The existence of source-sink dynamics between boreal forest and low-altitude meadow habitat appears to be implicated in the current prolonged low in the 10-year snowshoe hare (*Lepus americanus*) cycle due to sustained predation pressure in the boreal forest. The onset of the increase phase of the hare cycle is expected to relieve predation pressure on arctic ground squirrels due to prey switching and allow for the successful re-colonization of boreal forest habitat. This study provides empirical evidence for the existence of source-sink dynamics in wildlife populations.

Introduction

A single species can often occupy heterogeneous habitats resulting in differential demographic rates (Pulliam 2000). Embedded in the concept of spatial heterogeneity in demographic rates is source-sink theory which describes a species occupying at least two different habitat types, sources and sinks (Pulliam 1988, Leibold et al. 2004). In source habitat types, reproduction exceeds mortality and a surplus of dispersers is produced. Conversely, sink habitats exist where reproduction is less than mortality and a net flow of conspecific dispersal from nearby sources is required for persistence in the sink habitat. The source-sink model for population dynamics (Pulliam 1988) developed in response to a growing literature that provided evidence for variable demographic rates within the same species occupying different habitats. The existence of source-sink population dynamics has important implications for our understanding of wildlife population dynamics and for more practical reasons such as guiding conservation efforts (Brawn and Robinson 1996, Kristan 2003, Perlut et al. 2008, Kanda et al. 2009). Contrary to balanced dispersal models (McPeck and Holt 1992a, Lemel et al. 1997) where dispersal is balanced between habitats of different quality resulting in equalized fitness, the source sink model has provided valuable insight into the mechanisms underlying species residency in unsuitable habitat types. Source-sink theory has also been used to explain the existence of meta-populations (Hanski 1998) and to identify the significant impacts that spatial variation in demographic rates can have on both local and regional population dynamics (Breininger et al. 2009). Identifying source-sink dynamics has also been important for prioritizing contemporary conservation efforts designed to protect high quality source habitat for rare and threatened species (Lampila et al. 2009, Nappi and Drapeau 2009, Schooley and Branch 2009).

Our ability to effectively demonstrate source-sink dynamics in natural systems however has been hindered by a paucity of detailed demographic data for populations in different habitat types (Watkinson and Sutherland 1995, Johnson 2004, Peery et al. 2006). Diffendorfer (1998) found that in published papers claiming to identify source-sink dynamics, 25 of 28 studies did not provide data sufficient to test the source-sink model. Density data alone is often inadequate to differentiate between sources and sinks since it is difficult to distinguish habitats with a low carrying capacity from sink habitats (Dias 1996, Brooks 1997). Instead, differences in density, survival, reproduction and movements among habitats are needed to properly identify source-sink dynamics in wild animal populations.

Arctic ground squirrels (*Urocitellus parryii plesius*) in the southern part of their range occupy three distinct habitat types; boreal forest, low elevation meadows and alpine meadows, and thus are an excellent candidate to investigate the potential for source-sink population dynamics. Arctic ground squirrels have been studied extensively in the boreal forest in the Kluane region since 1990 (see Boutin et al. (1995), Hubbs and Boonstra (1997), Byrom and Krebs (1999), Karels and Boonstra (1999), Karels et al. (2000), Hik et al. (2001), Gillis et al. (2005)) and have been shown to fluctuate with the 10-year snowshoe hare cycle in response to shared predators (Boutin et al. 1995). Since 2000, arctic ground squirrel populations in the boreal forest have remained low and in some locations have been extirpated (Chapter 2, Gillis et al. 2005). Conversely, populations in alpine meadows appear to be larger and more stable than those in the boreal forest and limited by overwintering conditions rather than predation (Green 1977, Gillis et al. 2005). Little information exists for arctic ground squirrel populations in low elevation meadow habitat. This study is the first to compare arctic ground squirrel demographic rates in three different habitat types; boreal forest, low meadow and alpine meadow.

Here I compared three habitat types (boreal forest, low meadow and alpine meadow) to assess whether arctic ground squirrel populations in the Kluane Region exhibit demographic characteristics indicative of source-sink population dynamics. More specifically I investigate the following hypotheses: (1) High elevation alpine meadow habitats function as population sources that provide individuals to low elevation population sinks and alternatively (2) Low elevation habitats are characterized by two distinct habitat units, meadow (source) and boreal forest (sink) that display discrete demographic conditions independent of those at higher elevations.

Methods

Study Species Arctic ground squirrels occupy arctic tundra, alpine areas and the boreal forest of northwestern Canada and Alaska (Nadler 1977). The majority of arctic ground squirrel life history is occupied by an 8-9 month period of hibernation from late July/early August to late April/early May (Carl 1971, Lacey 1991). Females begin to breed almost immediately upon emergence in spring and produce one litter/year around 25 days later in mid-May (Green 1977, Lacey 1991, Lacey et al. 1997). Juveniles emerge from the natal burrow in mid/late June and begin to disperse in mid-July. Juvenile arctic ground squirrel dispersal has been shown to be highly male biased (Byrom and Krebs 1999).

Study Sites Arctic ground squirrels were studied in three different habitat types at five locations in the Kluane Region, Yukon Territory (Figure 5). More specifically they were studied at two locations in the boreal forest, one in low elevation meadow habitat and two in alpine meadow habitat. In the boreal forest, data were collected at two 10 ha study sites (~900 m asl [above sea level] (N 61° 00' 38'' W 138° 11' 31'' and N 60° 55' 53'' W 137° 58' 25'')) located ~20 km from each other (see Gillis et al. 2005). Both boreal forest grids were dominated by white spruce forest and willow thickets with occasional aspen stands. In low elevation meadow habitat (~800 m asl),

squirrels were studied in the Slims River valley in Kluane National Park and Reserve (KNPR), Yukon Territory, Canada. The low elevation meadow study site is located in south facing meadow habitat surrounded by boreal forest and by the Slims River delta immediately to the east (N 60°59'56'' W 138°33'31''). The first 12 ha alpine meadow study area (~1800 m asl) (N 61°10'57'' W 138°26'02'') was located ~30 km from the second alpine meadow study site in KNPR and consisted of open, south facing meadow habitat with bare ground and boulder fields (see Gillis et al. 2005). The second alpine meadow study area (~1600 m asl) was located in KNPR and ~8 km uphill from the low elevation meadow site in south facing alpine meadow habitat (N 61°01'06'' W 138°37'34''). Data for the boreal forest were compiled from Krebs et al. (2001), Gillis et al. (2005) and Krebs (2009, unpublished data). Data for low elevation meadow and alpine meadow habitat for 1975-1976 were compiled from Green (1977). Data for the first alpine meadow study area was compiled from Gillis et al.(2005).

All study areas lie within the rain shadow of the St. Elias Mountains and therefore the climate is characterized by cool, dry weather conditions (total annual precipitation ~280 mm, average annual temperature -3.8° C;(Environment Canada Canadian Climate Normals).

Trapping and Handling This research was approved by the University of British Columbia Animal Care Committee in accordance with the guidelines of the Canadian Council for Animal Care. In the boreal forest, arctic ground squirrels were trapped on two 10 ha grids with traps spaced 30 m apart in a 10x10 array with traps placed at alternate grid stakes. At the low elevation meadow site, squirrels were trapped on a 9ha grid with traps spaced 50 m apart in a 5x10 array with traps at each grid stake. At the first alpine meadow site, squirrels were trapped on a 12 ha grid with traps spaced 50 m apart in a 7x7 array with traps at each grid stake. At the alpine meadow site in KNPR, trapping occurred on a 9 ha grid with traps placed 50 m apart in a 7x7

array with traps at each grid stake. Squirrels were trapped using Tomahawk live traps (14 x 14 x 40 cm, Tomahawk live trap Co., Tomahawk, Wisconsin) baited with peanut butter and transferred to a mesh bag, tagged with monel No. 1005-1 tags (National Band and Tag Co., Newport, Kentucky) in both ears, weighed with a Pesola spring scale (± 5 g), sexed and measurements of skull width (± 0.5 mm) were taken.

Survival Female arctic ground squirrel survival was divided into active season and overwinter survival. Active season survival was calculated as the proportion of females caught in the spring trapping session that were re-caught in the fall trapping session. Over-winter survival was calculated as the proportion of females caught in the fall trapping session that were re-caught following spring. Only female ground squirrels were used in the survival analysis derived from trapping records because disappearance of males could not be distinguished from death vs. dispersal.

Juvenile Survival and Dispersal Radio telemetry was used to calculate active season survival and dispersal distances for juvenile arctic ground squirrels at both study areas in KNPR during the 2009 active season. A total of 34 juvenile arctic ground squirrels (17 low elevation meadow site, 17 alpine meadow site) were fitted with expandable 5g radio collars (PD-2C transmitters, Holohil Systems Limited, Carp, Ontario). Radio collars were fitted 1 week after emergence from the natal den and squirrels were located twice per week throughout the active season at each study site until late August. Travel distances were determined using a handheld GPS unit (Garmin GPSmap60cx, Olathe, Kansas) and measured as the straight line distance from the location of capture at emergence to late August when juveniles have finished dispersal (Green 1977, Lacey 1991, Byrom and Krebs 1999). To determine what habitat type juvenile arctic ground squirrels were moving to, the habitat type that was occupied during the last 3

locations for an individual in late August was used. To determine the habitat type for radio collared individuals that died, the habitat occupied for the last 3 locations was used.

Recruitment To compare recruitment between habitat type, an index was used and calculated as the ratio of juveniles to adult females captured in the fall trapping session of each year.

Population Growth Rate (λ) Population growth rates from fall to fall were calculated for each habitat type using reverse-time Pradel models (Pradel 1996) in program MARK v6.1 (White and Burnham 1999). Program MARK uses binary mark-recapture data to estimate survival rates, recapture probabilities and population growth rates (λ). Habitat specific mark-recapture data from fall trapping sessions was used and data were pooled for both sexes. For all models, survival (ϕ) and lambda (λ) were modeled as time-dependant while recapture probability (p) was time constrained. Since time constraints on survival (ϕ) and lambda (λ) values generally do not make biological sense and fully time dependant models result in the first and last λ values being inestimable (Franklin 2002), constraints were only placed on recapture probabilities. For further explanation of Pradel models in program MARK see Franklin (2002).

Statistical Analyses All data are given as means \pm SE. All statistical analyses were calculated using program JMP v4.0 (SAS institute, Cary, NC). Active season survival, overwinter survival and the ratio of juveniles to adults were analyzed using a one-way ANOVA with Tukey's post-hoc tests. Prior to analysis all data were assessed for normality and homogeneity of variance and either transformed or analyzed using non-parametric methods if these assumptions were not met. Juvenile dispersal distances did not meet the assumptions of normality and equal variance and were therefore analyzed using non-parametric methods. Survival (38-day) estimates for radio collared juvenile arctic ground squirrels were calculated using the Kaplan-Meier procedure (Pollock et al. 1989).

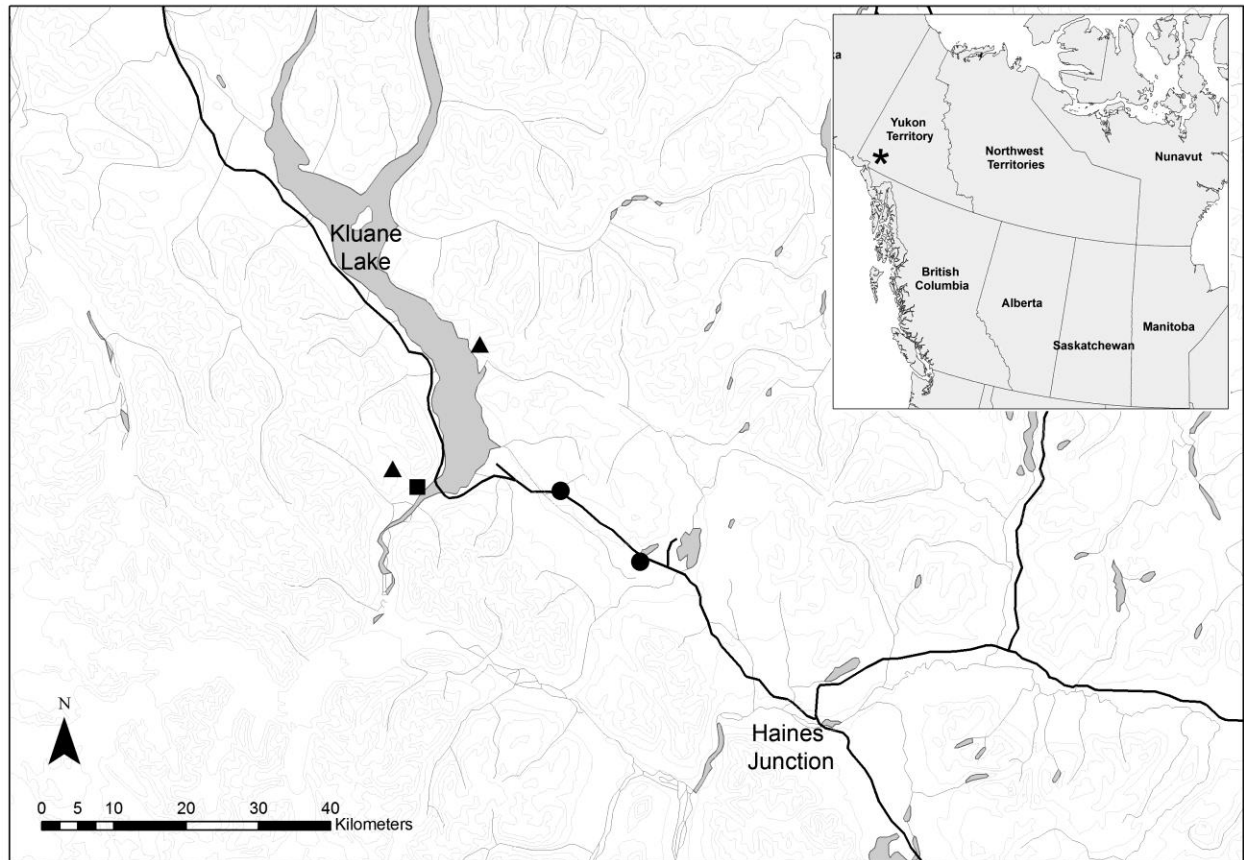


Figure 5 Study area location. Circles represent boreal forest trapping grids, squares represent low meadow trapping grids and triangles represent alpine meadow grids.

Results

Survival Female arctic ground squirrels in the boreal forest survived poorly ($43\% \pm 5$, $n=18$ years) over the 4 month active season compared to female arctic ground squirrels in both low elevation meadow ($73\% \pm 10$, $n=4$ years) and alpine meadow habitats ($80\% \pm 8$, $n=7$ years) ($F_{2,28}$, $P=0.001$) (Figure 6). No significant differences were observed in overwinter survival between habitat types ($F_{2,26}$, $P=0.23$) (Figure 7) although female arctic ground squirrels appear to survive better in boreal forest ($65\% \pm 5$, $n=16$ years) and low elevation meadow ($66\% \pm 9$, $n=4$ years) habitats than in alpine habitats ($51\% \pm 8$, $n=6$ years).

Juvenile Survival and Dispersal A total of 34 juveniles were radio collared in the summer of 2009. Kaplan-Meier 38-day survival estimates were calculated first for all males and females pooled and then for males only (Figures 8 and 9). Overall juveniles and male juveniles survived poorly in low elevation meadow habitat compared to alpine meadow habitat (all juveniles: 50% low vs. 92% high, log-rank test; $\chi^2=5.50$, $df=1$, $P=0.02$, $n=29$). When juvenile males are analyzed separately, the difference in survival between late summer survival in low and alpine meadow habitats is accentuated (male survival: 40% low vs. 90% high, log-rank test; $\chi^2=5.16$, $df=1$, $P=0.02$, $n=20$). Radio collared juveniles in low elevation meadow habitat also moved farther (Figure 10) than those in alpine meadow habitat (low meadow $319 \text{ m} \pm 71$ vs. alpine meadow $76 \text{ m} \pm 71$, Mann-Whitney U test, $\chi^2=10.40$, $df=1$, $n=27$, $p=0.001$). Sixty-five percent (8 males, 3 females) of juveniles in low elevation meadow habitat moved to boreal forest habitat and 73% of these were subsequently predated. Predation by either northern goshawk (*Accipiter gentillis*) or red-tailed hawk (*Buteo jamaicensis*) accounted for 100% of the mortalities in the boreal forest. All 6 individuals (3 male, 3 female) that remained in meadow habitat survived the

entire 38 day period from July 12th-August 19th. Radio collared juveniles in both low meadow and alpine meadows showed no movements between these habitats.

Recruitment Boreal forest habitat contained significantly fewer juveniles to adult females (0.44, SE±0.18, n=9 years) than both low meadow (1.14 ±0.11, n=4 years) and alpine meadow (1.41 ±0.26, n=10 years) habitat types ($F_{2,22}$, $P=0.01$) (Figure 11)

Population Growth Rate (λ) Estimates of population growth rates (λ) from fall to fall were 0.68 ± 0.2 (n=9 years), 0.90 ± 0.21 (n=1 year) and 0.98± 0.13 (n=1 year) for boreal forest, low meadow and alpine meadow habitats respectively. Population growth rates recorded from 1975-1976 at the same low meadow and alpine meadow study areas were 1.1 and 1.0 respectively.

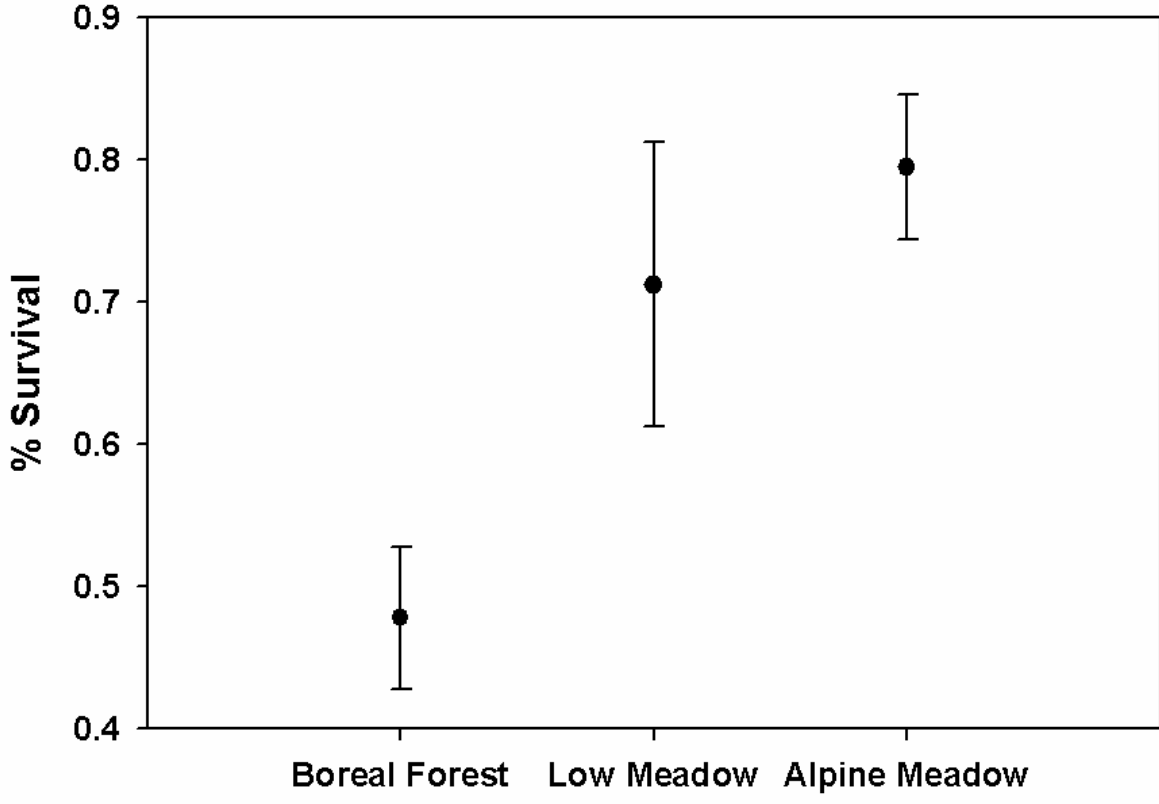


Figure 6 Female arctic ground squirrel active season survival. Bars represent 1 SE. Source: boreal forest data (Krebs 2009, unpubl.), low meadow/alpine meadow data 1975-1976 (Green 1977), alpine meadow data 2000-2002 (Gillis et al. 2005).

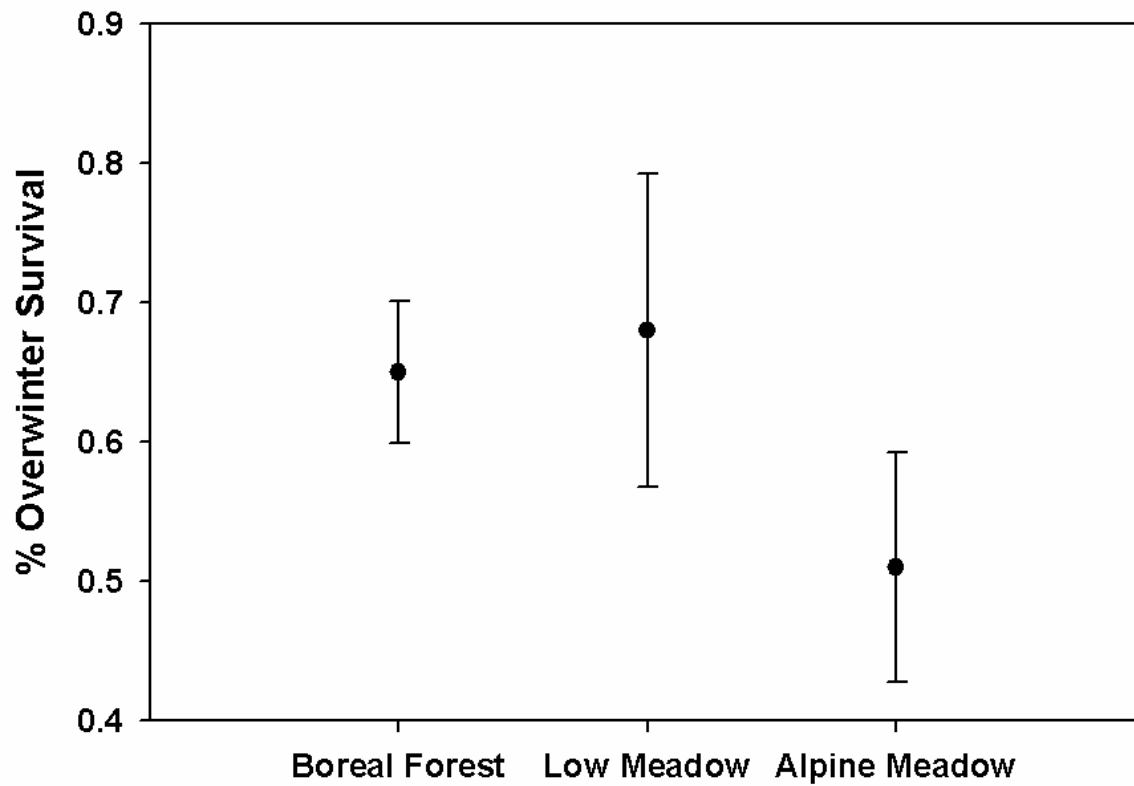


Figure 7 Female arctic ground squirrel overwinter survival. Bars represent 1 SE. Source: boreal forest (Krebs 2009 unpubl.), low meadow/alpine meadow 1975-1976 (Green 1977), alpine meadow 2000-2002 (Gillis et al. 2005).

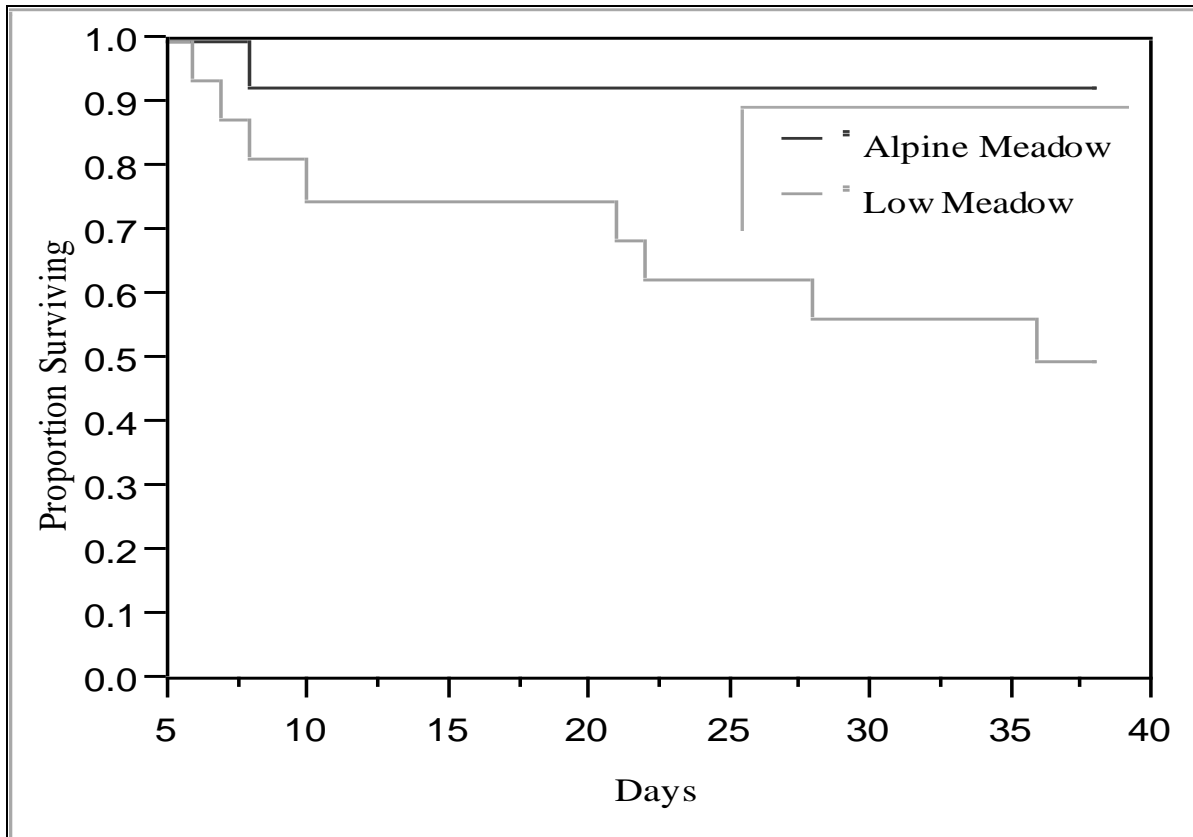


Figure 8 Kaplan-Meier 38-day survival curves for all radio collared juvenile arctic ground squirrels. (50% survival low vs. 92% alpine, log-rank test; $\chi^2=5.50$, $df=1$, $P=0.02$, $n=29$).

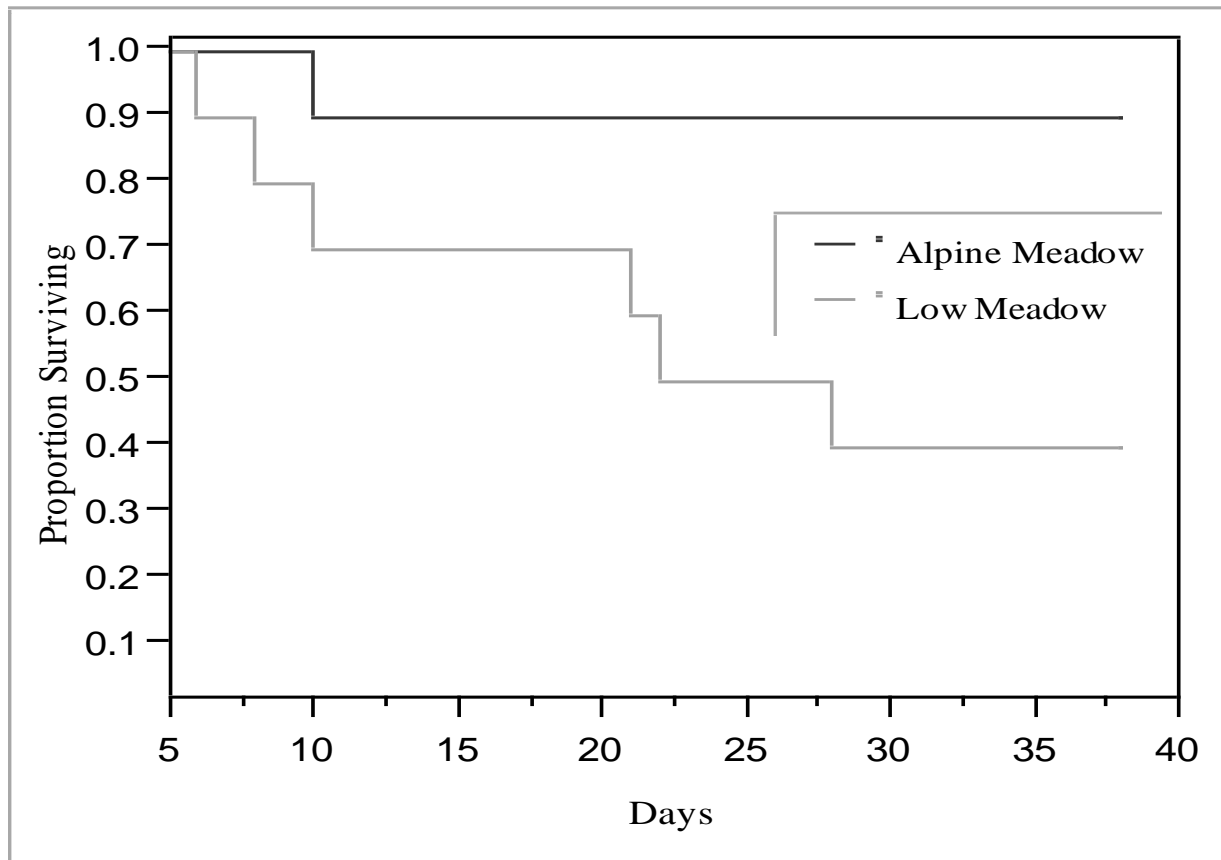


Figure 9 Kaplan-Meier 38-day survival curves for radio collared juvenile male arctic ground squirrels. (40% survival low vs. 90% alpine, log-rank test; $\chi^2=5.16$, $df=1$, $P=0.02$, $n=20$).

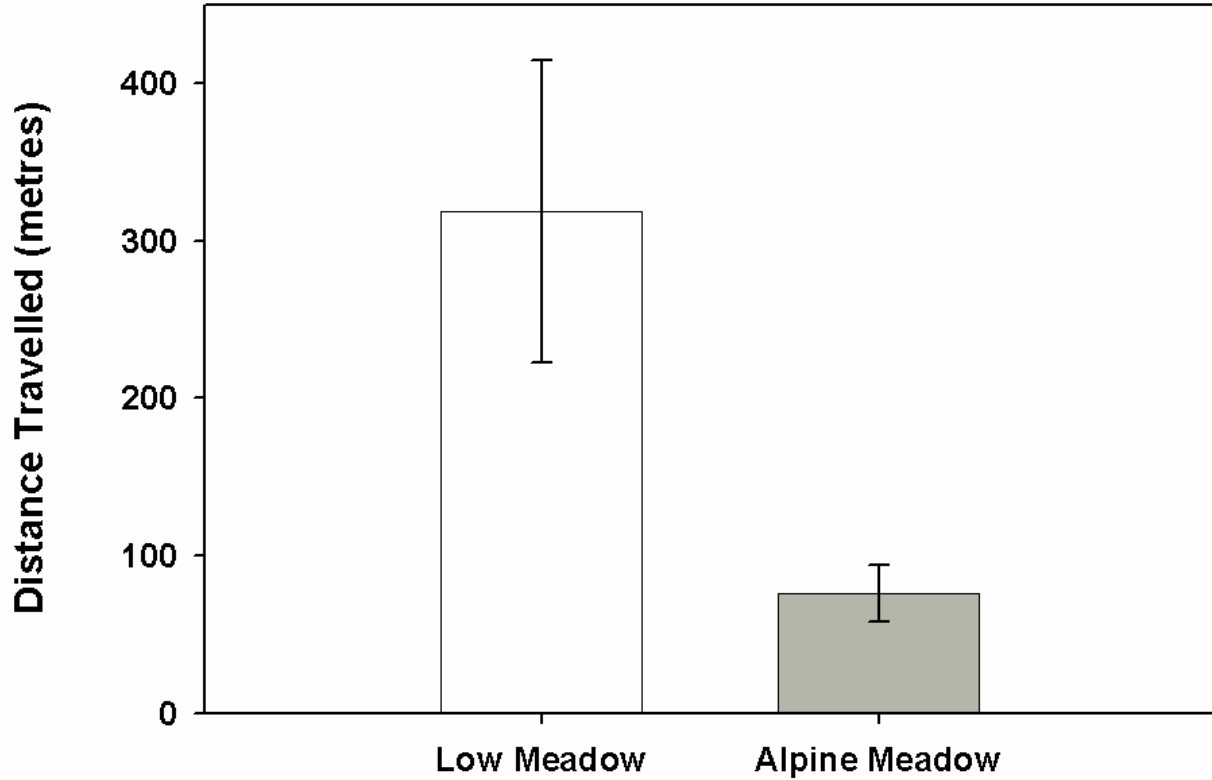


Figure 10 Distance moved by radio collared arctic ground squirrels in low elevation meadow and alpine meadow habitat. Bars represent 1 SE. (low meadow 319 m vs. alpine meadow 76 m, Mann-Whitney U test, $\chi^2=10.40$, $df=1$, $n=27$, $p=0.001$).

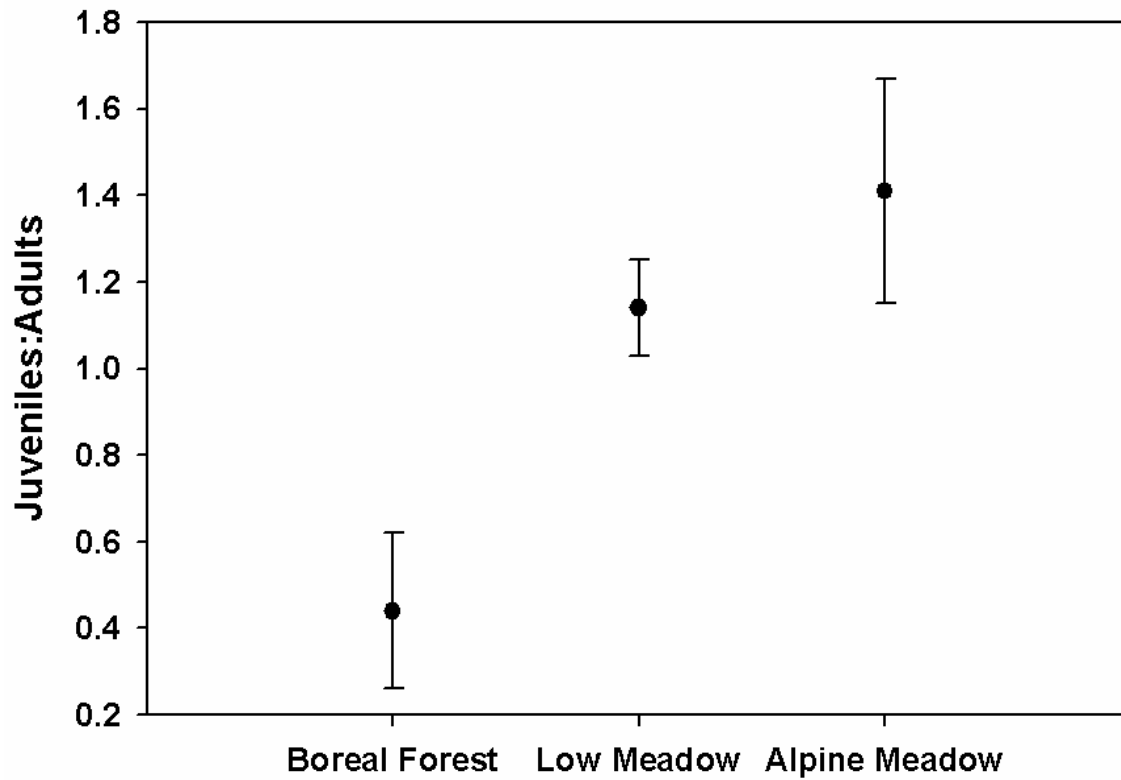


Figure 11 Recruitment rate (juveniles:adults) of arctic ground squirrels in three habitat types. Bars represent 1 SE. Source: boreal data (Krebs et al. 2009, unpubl.), low meadow/alpine meadow 1975-1976 (Green 1977), alpine meadow 2000-2002 (Gillis et al. 2005).

Discussion

My results support the hypothesis that arctic ground squirrels exhibit habitat specific demographic rates and that low elevation habitats appear to be characterized by two distinct habitat units, low meadow (source) and boreal forest (sink). Surprisingly, the demography of populations in low elevation meadows was more similar to alpine meadows than nearby boreal forests. Boreal forest arctic ground squirrel populations are smaller (Chapter 2) and experience demographic characteristics indicative of sink habitat types. The extirpation of ground squirrels from the boreal forest (Chapter 2, Gillis et al. 2005), poor active season survival, low recruitment rates, immigration from nearby low elevation meadow habitat and population growth rates <1.0 provide convincing evidence that the boreal forest functions as sink habitat for arctic ground squirrels.

Conversely, nearby arctic ground squirrel populations in low elevation meadow habitat appear to be stable and self sustaining and appear to function as population sources for populations in the boreal forest. Juveniles in this study moved from low elevation meadow habitat into boreal forest habitat which suggests that low elevation meadows have the capacity to support a nearby population sink. These findings also validate ideas presented by Gillis et al. (2005) suggesting that boreal forest populations are functioning as population sinks and that nearby meadow habitats may provide the immigrants required to sustain arctic populations in the forest.

Alpine meadow habitats support higher densities of arctic ground squirrels, exhibit higher active season survival rates and survive poorly overwinter compared with arctic ground squirrels in low elevation habitats. Animal movement data provides no support for the hypothesis that alpine meadow populations supplement low elevation populations. Radio-collared arctic ground squirrels in alpine meadow habitat moved very little suggesting that long distance

dispersal events between high and low elevations are rare and not sufficient enough to supply individuals to low elevation habitats.

Survival

The survival data suggests that active season is the most important limiting factor for arctic ground squirrels in the boreal forest. The poor active season survival of adult female arctic ground squirrels in the boreal forest compared to low elevation meadow habitat, the movement of radio-collared juveniles from low meadow habitat into nearby boreal forest habitat and the subsequent high incidence of predation, all suggest that top-down pressures are inhibiting the recovery of boreal forest arctic ground squirrel populations. Increased predation in the boreal forest is likely due to a number of factors including a reduced ability to detect and avoid predators in boreal forest habitat, a higher abundance of predators, the current prolonged low of the snowshoe hare (*Lepus americanus*) cycle and hence lack of alternative prey; and by the small ground squirrel population sizes themselves in this habitat type.

First, a small ground based herbivore requires good visibility to detect and avoid predators and communicate the presence of a predator to conspecifics. Both low elevation and alpine meadow habitats allow for increased predator detection (Gillis et al. 2005) as they are dominated by small grasses and forbs. Boreal forest habitats in the Kluane region are dominated by white spruce trees and other tall shrubs that likely reduce the ability of arctic ground squirrels to detect and evade predators (Karels and Boonstra 1999). Increased shrub density in the boreal forest has also been observed over the last 15 years (Krebs pers.comm), likely in response to climatic changes. Indeed, numerous other studies on ground squirrels and closely related marmot species have shown that habitats with reduced visibility result in increased predation rates, increased vigilance behavior and lower reproductive rates thereby facilitating high extinction

probabilities (Sharpe and Van Horne 1998, Byrom et al. 2000, Gillis et al. 2005, Blumstein et al. 2006, Ricankova et al. 2006, Mateo 2007). Hik et al. (2001) studying arctic ground squirrels in the same area found that squirrels in the boreal forest were more stressed than those living in open meadow habitats and that this difference in stress was likely indicative of increased predation risk in boreal forest habitat. They also suggest that these differences in stress can result in important demographic consequences such as reduced survival and recruitment in this habitat type. Data collected in this study and by Gillis et al. (2005) also show that reduced active season survival and reproductive rates are indicative of this habitat type. Byrom and Krebs (1999) also found that predation was responsible for 97% of juvenile arctic ground squirrel mortality in the boreal forest.

A second important factor influencing increased predation is simply that there are more predators in boreal forest habitat (Hik et al. 2001, Gillis et al. 2005). In addition to the dominant predators found in meadow habitats (red fox (*Vulpes vulpes*), golden eagles (*Aquila chrysaetos*), grizzly bear (*Ursus arctos*)), predators in the boreal forest also include the northern harrier (*Circus cyaneus*), red-tailed hawk, northern goshawk, great horned owl (*Bubo virginianus*) Canada lynx (*Lynx canadensis*) and coyote (*Canis latrans*) (Krebs et al. 2001). Given the close proximity of boreal forest habitat to low meadow habitat it is probable that a number of these species prey on arctic ground squirrels in low meadows as well. However the enhanced ability of squirrels in low meadow habitat to detect predators likely increases their ability to evade predation.

In the boreal forest arctic ground squirrel populations typically exhibit cyclical fluctuations that are positively correlated with the 8-10 year snowshoe hare cycle, but with a lag of 1-2 years (Boutin et al. 1995, Boonstra et al. 2001, Krebs et al. 2001) and this lag is likely due

to prey switching (Hubbs and Boonstra 1997). Arctic ground squirrel population sizes in the boreal forest started to decline in 1998 (Chapter 2) in response to the concurrent decline in snowshoe hare abundance, since ground squirrels are an alternative prey species, and have numbers have remained low from 1998 to the present. Snowshoe hare densities in the boreal forest began to increase again in 2004 with peak densities occurring in 2006, however the densities in 2006 were less than half of those observed during the previous peak in 1998 (0.92 hares/ha in the 2006 vs. 1.98 hares/ha in 1998 (Sheriff et al. 2009). During the increase and peak phases of the hare cycle the ability of arctic ground squirrels to successfully move from meadow habitat (source) into the boreal forest (sink) is likely facilitated by the increased abundance of the primary prey species in this habitat type, the snowshoe hare. During the low phase of the hare cycle however, the ability of arctic ground squirrels to colonize areas in the boreal forest is likely inhibited by intense predation. Boonstra et al. (2001) found that during the decline and low phase of the snowshoe hare cycle that the proportion of arctic ground squirrel in the diets of lynx, coyote, red fox, great horned owl and northern harrier all increased. Interestingly, the proportion of arctic ground squirrel in the diet of the dominant ground squirrel predators observed in this study, the northern goshawk and the red-tailed hawk, appears to remain relatively constant throughout all phases of the snowshoe hare cycle. Therefore, the increased predation by typical hare predators during the decline and low phases of the hare cycle coupled with sustained predation pressure from northern goshawks and red-tailed hawks is likely inhibiting the re-establishment of arctic ground squirrel populations in the boreal forest.

Lastly, arctic ground squirrels live in a network of social groups located in close proximity that consist of various females and usually one territorial male. Specialized alarm calls for both avian based and terrestrial predators within these social groups of ground squirrels

notify nearby members of impending threats. In meadow habitats, individuals can likely detect predators from further away and notify other members in the population sooner than individuals in the boreal forest. The enhanced ability of arctic ground squirrels in low elevation meadows to detect predators likely facilitates the persistence of low elevation meadow populations when compared to squirrels in the boreal forest. The importance of group vigilance behavior or the “many eyes” hypothesis in social animals has been well documented in the literature (Caraco et al. 1980, Kildaw 1995, Lima 1995, Roberts 1996, Fairbanks and Dobson 2007). The small populations in the boreal forest are therefore unlikely to detect predators as well as in meadows increasing their probability of extirpation in this habitat, a process that is possibly facilitated by an Allee effect (Allee 1931).

Although differences in arctic ground squirrel active season survival are pronounced and likely driving the population dynamics between habitat types, overwinter survivorship appears to also be an important limiting factor in all habitat types. Indeed, overwinter survivorship has been shown to be an important limiting factor for a number of hibernating rodents given a typical 8-9 month/year hibernation period (Murie and Boag 1984a, Schwartz et al. 1998, Buck and Barnes 1999a, Karels et al. 2000). The physiological demands associated with hibernation and variation in overwintering conditions make arctic ground squirrels in all three habitat types particularly susceptible to mortality during this life history stage. Changes associated with climatic warming may have pronounced effects on arctic ground squirrel persistence and the effects that winter rain events and warmer temperatures may have on overwinter survivorship needs to be further explored. The similar overwinter survivorship of arctic ground squirrels in all three habitats during this study however, suggests that overwintering conditions may not be the most

immediate factor explaining the decline of arctic ground squirrels in the boreal forest and also that predation rather than food limitation is driving the observed differences in demography.

Juvenile Survival and Dispersal

During this study, the downward migration of arctic ground squirrels from alpine meadows to lower elevation habitats was not observed providing evidence to temporarily reject the hypothesis that high elevation habitats function as population sources to low elevation population sinks. Another study investigating arctic ground squirrel dispersal in alpine meadow habitats also found no evidence for “downhill” migration (Gillis 2003). The movement of radio collared juveniles from low elevation meadow habitat into boreal forest and the subsequent high rate predation does however provide further evidence for the hypothesis that low elevation habitat may be characterized by two discrete units, sources (low elevation meadows) and sinks (boreal forest). Since adult females move very little (Karels and Boonstra 2000), the successful colonization of boreal forest is hinged upon the dispersal of juvenile arctic ground squirrels from low elevation meadow source habitats. During the increase and peak phase of the snowshoe hare cycle when hares comprise the majority of the diet for low elevation predators, the likelihood of successful boreal forest colonization by juvenile arctic ground squirrel dispersing from low meadow habitats would likely increase thereby providing an opportunity for populations in the boreal forest to re-establish. As previously discussed, during the decline and low phases of the snowshoe hare cycle it appears that successful colonization is inhibited by increased predation pressures.

Recruitment

The low recruitment rates observed in the boreal forest compared to those in low elevation meadow and alpine meadow habitat, suggest that arctic ground squirrel populations in

the boreal forest are either reproducing less, having smaller litter sizes, exhibiting lower juvenile survival or that potential recruits from nearby low meadow habitats are not able to successfully re-colonize boreal forest habitat. A combination of these factors is likely responsible for the observed low recruitment rates in the boreal forest and apart from the causation; boreal forest habitat contains fewer juvenile arctic ground squirrels than low and alpine meadow habitat types. Unfortunately, determining litter sizes and reproductive success for arctic ground squirrels is difficult since females are known to share natal dens (Lacey 1991). Data from this study however, show that juvenile active season survival in boreal forest habitat is lower than in low elevation meadow and alpine meadow habitats due exclusively to predation and that individuals moving from low meadow into the boreal forest are at high risk of predation, further inhibiting population growth in boreal forest habitat types.

Habitat specific recruitment rates are indicative of source-sink population dynamics and low recruitment rates have been used to identify sink populations in a variety of plant and animal studies (Eriksson 1996, Gundersen et al. 2001, Bruna 2003, Caudill 2003, Perlut et al. 2008). The low recruitment rates observed in boreal forest habitat in this study provide further support for the hypothesis that the boreal forest functions as sink habitat for arctic ground squirrels.

Population Growth Rate (λ)

Population growth rates provide support for the hypothesis that the boreal forest is functioning as a sink habitat type (i.e. $\lambda < 1$). Data collected over a 10 year period during all phases of the snowshoe hare cycle, show that population growth rates (λ) in this habitat types rarely exceed 1.0 with an average value of 0.68. Although the population growth rates presented here for both low elevation meadow and alpine meadow habitat only contain growth rates (λ) calculated in MARK for a one year period (2008-2009), when simplified population growth rates

(n_{t+1}/n_t) are calculated using data from Green (1977), who studied arctic ground squirrels at the same low elevation meadow and alpine meadow locations used for this study, rates of 1.0 or >1.0 are observed. It is difficult to interpret what has occurred between this 35 year time period (1975-2010) in both of these low elevation meadow and alpine meadow habitat types, however the persistence of arctic ground squirrels in these meadow habitat types and the simultaneous extirpation of ground squirrels from the boreal forest (Chapter 2), provides convincing evidence that the boreal forest is functioning as sink habitat for arctic ground squirrels.

Conclusion

My results presented here provide empirical support for the hypotheses that arctic ground squirrels exhibit habitat specific demographic rates and display characteristics indicative of source-sink population dynamics. Low elevation habitat appears to be characterized by two discrete habitat units; low elevation meadow habitat (sources) and the boreal forest (sink). The downward migration of arctic ground squirrels from alpine meadow habitat to low elevation habitats was not observed and therefore the alternative hypothesis that alpine meadow habitats function as population sources to low elevation sinks can be temporarily rejected. The source-sink dynamics associated with low elevation habitats (low meadows and boreal forest) appears to be implicated in the recent prolonged low in the snowshoe hare cycle. The relative absence of snowshoe hares from low elevation habitats has resulted in sustained predation pressures on an important alternative prey species at low elevations, the arctic ground squirrel. The structural characteristics associated with low elevation meadow habitat likely facilitate enhanced predator detection and avoidance compared to boreal forest habitat allowing for the sustained presence of arctic ground squirrel populations in low meadows. The onset of the increase phase of the snowshoe hare cycle expected over the next few years is therefore expected to relieve predation

pressure in low elevation ground squirrel habitat and allow for arctic ground squirrel populations to temporarily re-establish themselves in the boreal forest via dispersal from nearby meadow habitat as observed in this study. Scientists and managers studying arctic ground squirrels should therefore focus on the more stable populations found in low elevation and alpine meadow habitats to better monitor temporal changes in this species.

Future research should focus on the genetic relatedness of arctic ground squirrels in low meadow, alpine meadow and boreal forest habitat to further determine the level of connectivity between these habitat types. Experimental tests for source-sink dynamics could involve the isolation of arctic ground squirrels in both low meadow habitat and boreal forest habitat and subsequent monitoring of population persistence.

Chapter 4-Summary and Future Research Direction

The primary objectives of my research were:

- 1) To determine the distribution and abundance of arctic ground squirrels in different habitat types in the Kluane Region of the Yukon.
- 2) To assess whether arctic ground squirrels exhibit habitat specific demographic rates indicative of source-sink dynamics.

The major findings of this research were:

- 1) Arctic ground squirrel density and relative abundance differed significantly among three habitat types; boreal forest, low elevation meadow and alpine meadow. Average densities in these habitat types were $0.38 \pm 0.13(1 \text{ SE})/\text{ha}$ in the boreal forest, $1.25 \pm 0.22/\text{ha}$ in low elevation meadow and $5.7 \pm 0.22/\text{ha}$ in alpine meadow habitat. At the completion of this study in 2010, arctic ground squirrels were absent from boreal forest trapping grids.
- 2) Arctic ground squirrel populations in northwestern Canada displayed population dynamics indicative of source-sink dynamics. Low elevation meadow habitat appears to function as a population source while boreal forest habitat exhibited demographic characteristics indicative of a sink habitat type. The existence of source-sink dynamics between these habitat types appears to be implicated in the 10 year snowshoe hare cycle in the region. During the low phase of the snowshoe hare cycle, the dispersal of juveniles from low elevation meadow habitat to boreal forest habitat is impeded by intense predation pressures by species using arctic ground squirrels as alternative prey in the absence of snowshoe hares and by more generalist predator species. The onset of the increase phase of the snowshoe hare cycle in 2011-2013 should relieve predation

pressures on dispersing juveniles and thereby facilitate the successful re-colonization of boreal forest habitat.

The findings of this study suggest the following future research would be useful for increasing our understanding of arctic ground squirrel demography in the Kluane region:

- 1) Analysis of the genetic relatedness of arctic ground squirrels in boreal forest, low elevation meadows and alpine meadows to further elucidate the possible genetic consequences of the source-sink dynamics observed in this study.
- 2) Demographic comparison during the increase and peak phase of the snowshoe hare cycle.
- 3) Experimental isolation of populations in low elevation meadows and the boreal forest and subsequent monitoring of population persistence.
- 4) Comparative analysis of body weight/condition upon emergence of hibernation and through the active season to determine if differences in food availability and overwintering conditions exist between habitat types.

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Appendix A

Effect of Habitat Type on Body Weight and Condition in Arctic ground squirrels (*Urocitellis parryi plesius*).

Introduction

Differences in body weight and body condition between populations of conspecifics have important implications for survivorship, reproduction and disease immunity in wildlife populations. Both body weight and body condition relate to the energetic state of an individual and have important fitness consequences. For species that hibernate, body weight at emergence/emergence and spring body condition are important determinants of overwinter survivorship, reproductive success and susceptibility to disease. Not surprisingly, the positive relationship between body mass/condition and overwinter survivorship in hibernating mammals has been well documented in the literature (Armitage et al. 1976, Young 1976, Armitage 1981, Murie and Boag 1984b, Neuhaus 2000). Variation in body mass and condition is also implicated in the reproductive success of hibernating mammals. Individuals that weigh more at emergence and emerge in superior spring body condition reproduce more frequently and have larger, more successful litters (Rieger 1996, Eva et al. 1999, Neuhaus 2000). Individuals in better body condition also appear to have an increased resistance to disease. For example, plague has been found to be the major factor responsible for the decline of black-tailed prairie dog populations in North America and individuals in superior body condition comprised a significant majority of survivors (Pauli et al. 2006). Regardless of the mechanism, differences in body weight and condition between wildlife populations can have important population level consequences and facilitate the habitat specific demographic rates indicative of source-sink dynamics. Source-sink theory, originally described by Holt (1985) but formalized by Pulliam

(1988), was developed to explain the existence of habitat specific demographic rates in wildlife populations. In source-sink theory, a species occupies at least two different habitat types where a disparity in demographic rates exists. More specifically, a species occupies source habitat types and sink habitat types. Source habitat types exist where births outnumber deaths allowing for a surplus of dispersers. Conversely, in sink habitat types, deaths outnumber births and persistence would not be possible without immigration from nearby source habitats

In this chapter I compare body weight and body condition of arctic ground squirrel (*Urocitellus parryii plesius*) populations in two different habitat types in source and sink habitat types in the boreal region of northern Canada. Arctic ground squirrels in this region occupy a variety of habitat types including the boreal forest, low elevation meadows and alpine meadows. Arctic ground squirrels in boreal forest habitat typically fluctuate with the 10-year snowshoe hare cycle in the region due to prey switching (Boutin et al. 1995). During the increase and peak phases of the hare cycle, the snowshoe hare comprises the primary prey species. However, during the decline and low phases of the snowshoe hare cycle, arctic ground squirrels become an important alternative prey species resulting in a 1-2 year lagged population decline. Upon the initiation of the increase phase of the hare cycle, ground squirrel numbers in the boreal forest typically increase again due to relieved predation pressure. Conversely, populations in nearby low elevation meadow habitats and at higher elevation in alpine meadows are larger and appear to remain stable (Chapter 2, Green 1977, Gillis et al. 2005). At the onset of the snowshoe hare decline in 1999, arctic ground squirrel populations in the boreal forest expectedly declined but have recently gone extinct while populations in low elevation meadow and alpine meadow habitats have persisted (Chapter 2). A study comparing demographic rates in all three habitat types found evidence that arctic ground squirrel populations in the southwest Yukon Territory

display source-sink dynamics where low elevation meadow habitats appear to function as population sources for boreal forest population sinks (Chapter 3). In this chapter I explore components of arctic ground squirrel fitness in source and sink habitat by comparing populations in boreal forest and low elevation meadow habitat to determine if arctic ground squirrels in sink habitat (boreal forest) weigh less and are in poor body condition compared with ground squirrels in source habitat (low elevation meadow). More specifically I test the following hypotheses: (1) arctic ground squirrels in boreal forest habitat weigh less at emergence in spring and immergence into hibernation in fall than ground squirrels in low elevation meadow habitat and that (2) arctic ground squirrels in boreal forest habitat are in poor body condition compared to ground squirrels in low elevation meadow habitat.

Methods

Study Species Arctic ground squirrels occupy arctic tundra, alpine areas and the boreal forest of northwestern Canada and Alaska (Nadler 1977). The majority of arctic ground squirrel life history is occupied by an 8-9 month period of hibernation from late July/early August to late April/early May (Carl 1971, Lacey 1991). Females begin to breed almost immediately upon emergence in spring and produce one litter/ year around 25 days later in mid-May (Green 1977, Lacey 1991, Lacey et al. 1997). Juveniles emerge from the natal burrow in mid/late June and begin to disperse in mid-July. Juvenile arctic ground squirrel dispersal has been shown to be highly male biased (Byrom and Krebs 1999).

Study Area Arctic ground squirrels were studied in two distinct habitat types, boreal forest and low elevation meadow habitat in the Kluane Region of the Yukon Territory, Canada. In the boreal forest, data were collected at two 10 ha study sites (~900 m asl [above seal level]) (N 61° 00' 38'' W 138°11'31'' and N 60°55'53'' W 137°58'25'') located ~20 km from each other (see

Gillis et al. 2005). Both boreal forest grids were dominated by white spruce forest and willow thickets with occasional aspen stands. In low elevation meadow habitat, data were collected in Kluane National Park and Reserve (KNPR). The 10 ha study site (~800 m asl) was located in the Slims River valley in south facing meadow habitat dominated by grasses and surrounded by boreal forest and by the Slims River delta immediately to the east (N 60°59'56'' W 138°33'31''). Data for the boreal forest were compiled from Krebs (2009, unpublished data).

Trapping and Handling This research was approved by the University of British Columbia Animal Care Committee in accordance with the guidelines of the Canadian Council for Animal Care. In the boreal forest, arctic ground squirrels were trapped on 10 ha grids with traps spaced 30m apart in a 10x10 array with traps placed at alternate grid stakes. At the low elevation meadow site, squirrels were trapped on a 9 ha grid with traps spaced 50 m apart in a 5x10 array at each grid stake. Squirrels were trapped using Tomahawk live traps (14 x 14 x 40 cm, Tomahawk live trap Co., Tomahawk, Wisconsin) baited with peanut butter and transferred to a mesh bag, tagged with monel No. 1005-1 tags (National Band and Tag Co., Newport, Kentucky) in both ears, weighed with a Pesola spring scale ($\pm 5g$), sexed and measurements of skull width ($\pm 0.5mm$) were taken.

Body weight and condition Average body weight was calculated for adult female ground squirrels upon emergence in spring (early-mid May) and just prior to hibernation in late summer of each year (early-mid August). Adult female spring (mid-May) body condition was calculated by comparing the residuals of body mass regressed on zygomatic arch width (skull width).

Statistical analyses.- All data are given as means \pm SE. Emergence and immergence weights were analyzed using a two sample t-test. All statistical analyses were calculated using program JMP v4.0 (SAS institute, Cary, NC). Prior to analysis all data were assessed for normality and

homogeneity of variance and either transformed or analyzed using non-parametric methods if these assumptions were not met. To determine the body condition of adult female arctic ground squirrels, I obtained the residuals of body mass (g) regressed on skull width (body mass=skull width) using simple linear regression. In a recent review assessing various methods of determining body condition, the ordinary least squares regression method to obtain residuals performed best (Schulte-Hostedde et al. 2005). This method of assessing body condition using the residuals of body mass regressed on skull size has also been used by various other ground squirrel researchers (Dobson and Michener 1995, Karels 2000) to assess female spring body condition. I then used this metric of body condition in a second model to investigate the effects of habitat and season on adult female arctic ground squirrel body condition (body condition=habitat).

Results

Body weight Arctic ground squirrels in both habitat types emerged in spring at a low body mass and accumulated mass before emergence into hibernation. Adult female arctic ground squirrels in low elevation meadow habitat were significantly heavier in spring ($437 \text{ g} \pm 11$) than squirrels in the boreal forest ($405 \text{ g} \pm 7$). ($df=55$, $t=2.40$, $P=0.02$). No differences were detected in adult female body weight in fall ($df=42$, $t=0.07$, $P=0.94$) (Figure 1). Average fall body weights were $520 \text{ g} \pm 15$ in low elevation meadow habitat and $519 \text{ g} \pm 13$ in the boreal forest (Figure 1).

Body condition The first model using adult female body weight regressed on skull width was significant ($y=11.05x+26.23$, $r^2=.10$, $n=69$, $F=6.57$, $P=0.01$). The second regression model using the residuals of body mass regressed on skull width (body condition = habitat) was also significant ($r^2=.11$, $n=69$, $F=6.1$, $P=0.01$). The results of the regression analysis are displayed in figure 2. Based on these two models, female arctic ground squirrels in boreal forest habitat are in

inferior body condition at emergence in spring than squirrels in low elevation meadows (df=68, t=2.47, P=0.01).

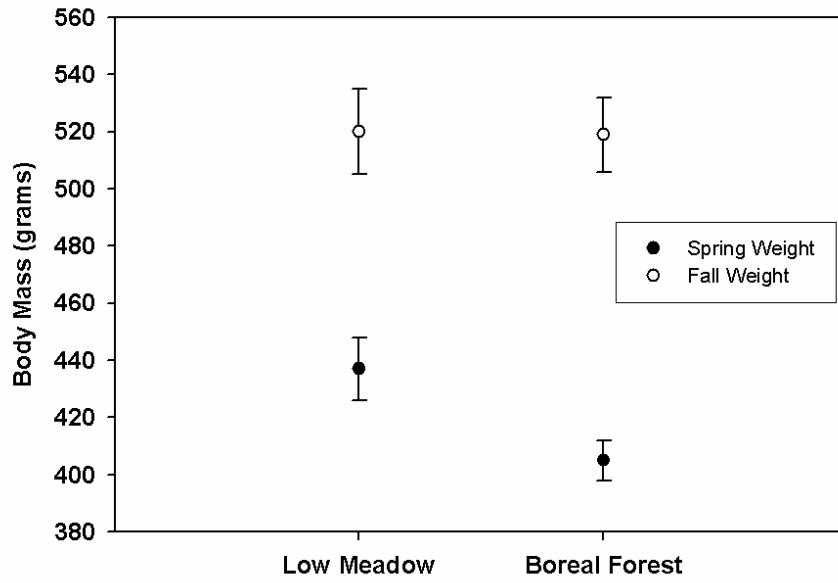


Figure A1 Adult female arctic ground squirrel spring and fall body mass. Bars represent 1 SE (Spring: 437 g low meadow, 405 g boreal forest. Fall: 520 g low meadow, 519 g boreal forest; t-test: $df=55$, $t=2.40$, $P=0.02$)

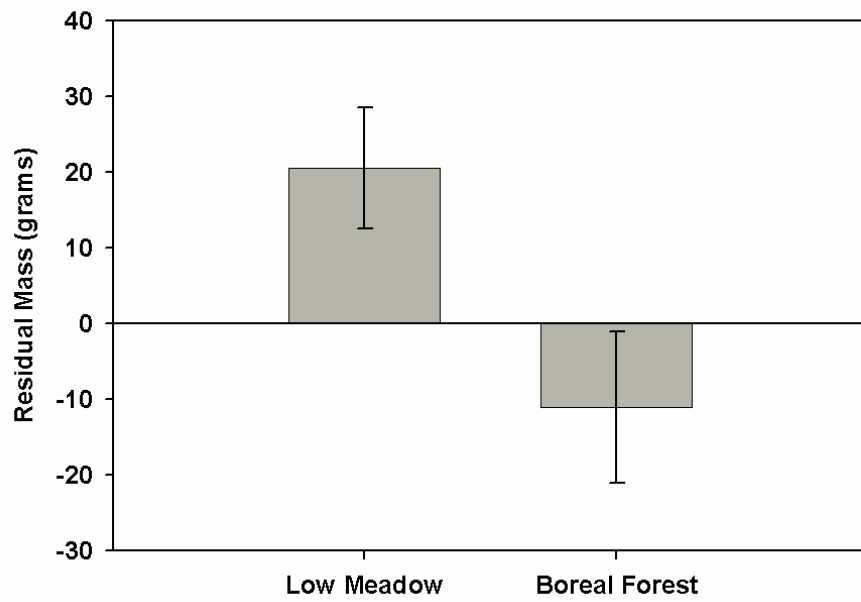


Figure A2 Adult female arctic ground squirrel spring body condition. Bars represent 1 SE (low meadow: 20.5 g, boreal forest: -11.0 g; t-test: $df=68$, $t=2.47$, $P=0.01$)

Discussion

Body Weight

These results show that adult female arctic ground squirrels in sink habitat (boreal forest) weigh significantly less at emergence than squirrels in source habitats (low elevation meadows) although by the onset of immergence into hibernation the observed body weight deficit between these habitat types has been recouped. The demographic implications of low emergence weight include low reproductive success, small litter sizes and increased overwinter survival since lighter individuals are unlikely to bear the energetic costs of reproduction. Indeed, low emergence mass in ground squirrels has been implicated in longer periods to ovulation, later weaning dates and smaller litter sizes (Millesi et al. 1999). Reiger (1996) also showed that the emergence weight of adult female Unita ground squirrels (*Spermophilus armatus*) was positively correlated with litter mass and litter size. Similarly Neuhaus (2000) studying Columbian ground squirrels (*Spermophilus columbianus*) showed that females that were lighter at emergence did not reproduce and were more likely to lose their litters but showed increased overwinter survival. These findings support those presented in Chapter 3 which show increased overwinter survival and a lower number of juveniles per adult females in the boreal forest compared to low elevation meadow habitats. The ability of arctic ground squirrels in the boreal forest to recoup the adult female weight deficit observed in spring also suggests that differences in resource availability may not be driving the source-sink dynamics observed between low elevation meadow and boreal forest habitat types. Although, large-scale experimental research on arctic ground squirrels in boreal forest habitat found that food addition increased densities to 4-7 times those observed on control plots (Karels et. al. 2000), it appears that in this study, differences in food availability may be negligible between habitats and may not be a factor driving the source-sink dynamics observed in this species. It appears that ground squirrels in the boreal forest were able

to gain enough mass so that by the onset of hibernation squirrels in both habitats weighed nearly the same.

Body Condition

These body condition results support the hypothesis that arctic ground squirrels in sink habitat (boreal forest) emerge in poor spring body condition compared to squirrels in source habitat (low elevation meadows). Differences in female ground squirrel body condition can have pronounced population level consequences directly by reduced survivorship and indirectly through reduced reproductive rates. Dobson and Michener (1995) studying Richardson's ground squirrels found that females in better body condition produced larger litter sizes. Similarly, Dobson et al. (1999) studying Richardson's ground squirrels (*Spermophilus richardsonii*) found that females in superior body condition produced more young and that females from these larger litter sizes. Individuals in poor body condition can also be more vulnerable to predation, particularly if the species is a secondary prey item that is more difficult to capture than a primary prey species. Wirsing et al. (2002) studying red squirrels in Idaho (*Tamiasciurus hudsonicus*) in a system where snowshoe hares are also the primary prey species that red squirrels in poor body condition were more intensely predated. Arctic ground squirrels in the boreal forest, which are also a secondary prey item in the boreal forest and where snowshoe hares also represent the dominant prey species, are in poor body condition and experience higher rates of active season mortality due to predation (Chapter 3). In Columbian ground squirrels, the closest relative of the arctic ground squirrel, females in superior body condition also have more successful and heavier litters that exhibit increased survival (Skibieli et al. 2009) These findings are also supportive of those data for arctic ground squirrels, that show increased densities, recruitment and survival rates in source habitats for females that are in superior body condition (Chapters 2 and 3)

The difference in adult female spring body condition observed here appear to be implicated in overwinter weight loss since squirrels in both habitat types weight nearly the same at immergence into hibernation. Arctic ground squirrels in boreal forest habitat may experience higher physiological demands associated with hibernation resulting in poor spring body condition and the suppressed demographic traits discussed above may manifest themselves through the source-sink dynamics observed in this species. For hibernating ground squirrels, soil temperature increases with snow depth and is negatively correlated with overwinter weight loss (Buck and Barnes 1999b). Differences in hibernacula quality between habitat types may therefore be responsible for the differences in spring body condition observed in this study. Karels (2000) studying arctic ground squirrels on the same grids in the boreal forest at Kluane found that open areas comprised 23% of the habitat in the boreal forest and that ground squirrels targeted these areas for hibernation since snow accumulation was greater and soil temperatures were warmer. Since boreal forest habitat is dominated by spruce trees and open areas comprise a small proportion of available habitat, a lack of high quality hibernacula in the boreal forest habitat may be responsible for the observed differences in spring body condition. Also, female ground squirrels move very little and tend to use the same burrows throughout their lifespan (Byrom and Krebs 1999). Since densities in the boreal forest are already low and females re-use hibernacula in close proximity, the consequences of an individual occupying a poor quality hibernaculum in the boreal forest are much greater than in low elevation meadow habitats. Conversely, since low elevation meadow contain higher densities, very few trees and are dominated by open areas the availability of quality hibernacula is likely greater, reducing the energetic costs of hibernation resulting in the observed superiority in female spring body condition in this habitat type.

Conclusion

The observed differences in adult female arctic ground squirrel emergence weight and spring body condition are likely implicated in the source-sink dynamics observed between arctic ground squirrels in the boreal forest and low elevation meadow habitats. Low emergence weight and inferior body condition has been shown to be associated with reduced reproductive output and reduced active season survival, demographic traits that are characteristic of arctic ground squirrels in boreal forest habitat. A limited availability of high quality hibernacula, resulting in increased physiological demands associated with hibernation, may be responsible for the observed differences in adult female spring body condition. It is likely that the increased predation pressure in boreal forest habitat in concert with inferior overwintering conditions are responsible for the source-sink dynamics observed between low elevation meadow and boreal forest habitats. Future work should compare hibernacula location and quality and associated survivorship between low elevation meadow and boreal forest habitat.

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