Habitat-specific distribution and abundance of arctic ground squirrels (*Urocitellus parryii plesius*) in southwest Yukon

S.A. Donker and C.J. Krebs

Abstract: Arctic ground squirrels (*Urocitellus parryii plesius* (Osgood, 1900); formerly *Spermophilus parryii plesius* Osgood, 1900) were studied in three distinct habitat types (boreal forest, low-elevation meadows, and alpine meadows) in the Kluane region of the southwest Yukon Territory, Canada, from 2008 to 2010 to determine if populations in these different habitats provide evidence for habitat-specific distribution and abundance. Abundance in the boreal forest has been shown to be synchronous with the cycle of snowshoe hares (*Lepus americanus* Erxleben, 1777) in the region owing to shared predators. We predicted that populations in the boreal forest would be low because of the current low phase in the cycle of snowshoe hares, and that in low-altitude meadows and alpine meadows, ground squirrels would be relatively abundant. Late-summer densities differed significantly between habitat types with 0.38 ± 0.13 squirrel/ha (mean ± 1 SE) in boreal-forest habitat, 1.25 ± 0.22 squirrel/ha in low-altitude-meadow habitat, and 5.7 ± 0.22 squirrels/ha in alpine-meadow habitat. In 2009, populations were extirpated from boreal-forest habitat, while densities in low-elevation meadows and alpine meadows were 1.6 ± 0.34 squirrel/ha and 6.1 ± 0.7 squirrels/ha, respectively. The current absence of squirrels from the boreal forest and the persistence of populations in low-elevation-meadow and alpine-meadow habitat suggest that source–sink dynamics may exist between boreal-forest and meadow habitat types.

Résumé : Nous avons étudié les sousliks arctiques (*Urocitellus parryii plesius* (Osgood, 1900); antérieurement *Spermophilus parryii plesius* Osgood, 1900) dans trois types d'habitat distincts (la forêt boréale, les prairies de basse altitude et les prairies alpines) dans la région de Kluane dans le sud-ouest du territoire du Yukon, Canada, de 2008 à 2010, afin de déterminer si les populations de ces différents habitats présentaient des répartitions et des abondances spécifiques aux habitats. On a démontré que leur abondance dans la forêt boréale est synchronisée avec le cycle des lièvres d'Amérique (*Lepus americanus* Erxleben, 1777) dans la région à cause de leurs prédateurs communs. Nous avons prédit que les populations dans la forêt boréale devraient être basses à cause du minimum actuel dans le cycle des lièvres d'Amérique, mais que les sousliks devraient être relativement abondants dans les prairies de basse altitude et les prairies alpines. Les densités en fin d'été différaient significativement entre les divers types d'habitats, avec 0,38 ± 0.13 souslik/ha (moyenne ± 1 ES) dans l'habitat de forêt boréale, 1,25 ± 0,22 souslik/ha dans l'habitat de prairie basse et 5,7 ± 0,22 sousliks/ha dans l'habitat de prairie alpine. En 2009, les populations ont été extirpées de l'habitat de forêt boréale, alors que les densités dans les prairies de basse altitude et les prairies alpines étaient respectivement de 1,6 ± 0,34 souslik/ha et de 6,1 ± 0,7 sousliks/ha. L'absence actuelle de sousliks dans la forêt boréale et la persistance des populations dans les prairies de basse altitude et les prairies alpines laissent croire à l'existence d'une dynamique de type source–puits entre les types d'habitats de forêt boréale et de prairie.

[Traduit par la Rédaction]

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; Kareiva et al. 1990; Pulliam 2000; Breininger et al. 2009; Krebs 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 models predict how animals move between habitat types and the demographic consequences of these movements, the balanced dispersal model (McPeek and Holt 1992) and the source–sink model (Pulliam 1988). The balanced dispersal model by McPeek and Holt (1992) describes a situation whereby the fitness of populations occupying different habitat types should eventually equalize, thereby negating the existence of habitat-specific demographic rates. McPeek and Holt (1992) and later Mobæk 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 mean fitness over time is compromised. In the balanced dispersal model, a situation prevails where habitats of varying carrying capacity exist over the landscape and the movement of animals between habitat types becomes "balanced" resulting in equal fitness in different habitat types (Diffendorfer 1998).

Source–sink theory, originally described by Holt (1985) but

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S.A. Donker and C.J. Krebs. Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

Corresponding author: C.J. Krebs (e-mail: krebs@zoology.ubc.ca).

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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 metapopulation dynamics first described by Levins (1969). Metapopulation 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 ordinarily experience extinction events.

Arctic ground squirrels (*Urocitellus parryii plesius* (Osgood 1900); formerly *Spermophilus parryii plesius* Osgood, 1900) provide the opportunity to investigate the empirical potential of the balanced dispersal and the source–sink models in wildlife populations. Arctic ground squirrels occupy a large geographic range mostly occupied by arctic tundra and alpine meadows in North America and Siberia (Nadler and Hoffmann 1977). Populations of arctic ground squirrels in arctic tundra and alpine meadows support high densities, remain stable, and appear to be limited by predation and burrow availability (Carl 1971; Green 1977; Buck and Barnes 1999). 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 squirrels in boreal-forest habitat (Byrom et al. 2000; Karels et al. 2000; Krebs et al. 2001; but see Green 1977 and Gillis et al. 2005). Boutin et al. (1995) have shown that densities of arctic ground squirrels in the boreal forest of the southwest Yukon are positively correlated with the densities of snowshoe hares (*Lepus americanus* Erxleben, 1777) (Pearson's $r = 0.69$) likely owing to shared predators, and this correlation remained strong until 2002. Populations of arctic ground squirrels in the boreal forest have been studied in the southwest Yukon since 1990, with densities ranging from 3.3 squirrels/ha during the peak of the cycle of snowshoe hares to 0.4 squirrels/ha during the low phase of the cycle of snowshoe hares (Boutin et al. 1995; Gillis et al. 2005). Because the majority of studies in the Kluane Region have focused on arctic ground squirrels in the boreal forest, relatively little is known about populations of arctic ground squirrels occupying both low-elevation meadows and alpine meadows.

Here we assess the current distribution and abundance of arctic ground squirrels by measuring density and relative abundance in three different habitat types. We measured population density by extensive livetrapping in low-elevation-meadow and alpine-meadow habitats from 2008 to 2010. Density data were also compiled from Green (1977) studying arctic ground squirrels in the same low-elevation-meadow and alpine-meadow sites that we used for this study. We compared these density data to data from Krebs et al. (2010), who studied arctic ground squirrels in boreal-forest habitat. We also used a powder tracking technique to assess the relative abundance of arctic ground squirrels in boreal forests, low-elevation meadows, and alpine meadows in other areas of the Kluane region. We hypothesized that the density and relative abundance of arctic ground squirrels in the Kluane region would be more indicative of the source–sink model rather than the balanced dispersal model. More specifically, we predicted that although density in the boreal forest is likely low because of intense predation pressure associated with the current low densities of snowshoe hares (Sheriff et al. 2009), the density of arctic ground squirrels in nearby low-elevation meadows and alpine meadows would be relatively abundant.

Materials and methods

Study species

The majority of the life history of the arctic ground squirrel life 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. Dispersal of juvenile arctic ground squirrels has been shown to be highly male-biased (Byrom and Krebs 1999).

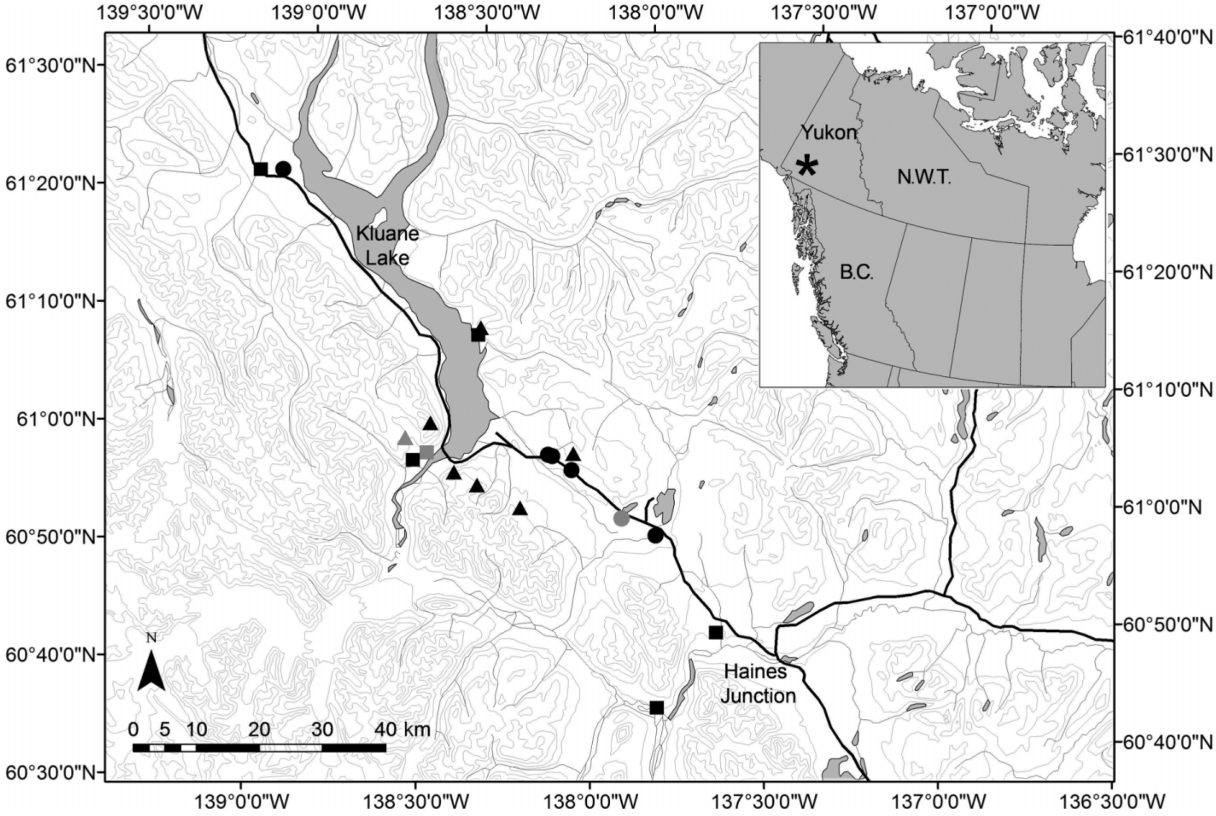
Study area

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 (Fig. 1). Detailed density data were collected at four locations. In the boreal forest, data were collected at two 10 ha study sites (~900 m above sea level (asl)) (61°00′38″N, 138°11′31″W and 60°55′53″N, 137°58′25″W, respectively) located ~20 km from each other (see Gillis et al. 2005). Both boreal-forest grids were dominated by white spruce (*Picea glauca* (Moench) Voss) forest and willow (genus *Salix* L.) thickets with occasional aspen (genus *Populus* L.) 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 the southfacing meadow habitat surrounded by boreal forest and by the Slims River delta immediately to the east (60°59′56″N, 138°33′31″W). 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 the southfacing alpine-meadow habitat (61°01′06″N, 138°37′34″W). Data for the boreal forest were compiled from Krebs et al. (2001), Gillis et al. (2005), and Krebs et al. (2010). Additional data for low-elevation-meadow and alpine-meadow habitats 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 on Animal Care. In the boreal forest, arctic ground squirrels were livetrapped on a 10 ha grid with traps spaced 30 m apart in a 10 × 10 array with

Fig. 1. Locations of arctic ground squirrels (*Urocitellus parryii plesius*) in the study area. The three habitat types are boreal forest (circles), low-elevation meadow (squares), and alpine meadow (triangles). The grey-shaded circle, square, and triangle represent areas where both density and relative abundance measures were taken. The black circles, squares, and triangles indicate areas where only indices of relative abundance were obtained.



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 5 × 10 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 7 × 7 array with traps at each grid stake. Squirrels were trapped using Tomahawk live traps (14 cm × 14 cm × 40 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) 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, USA) 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.

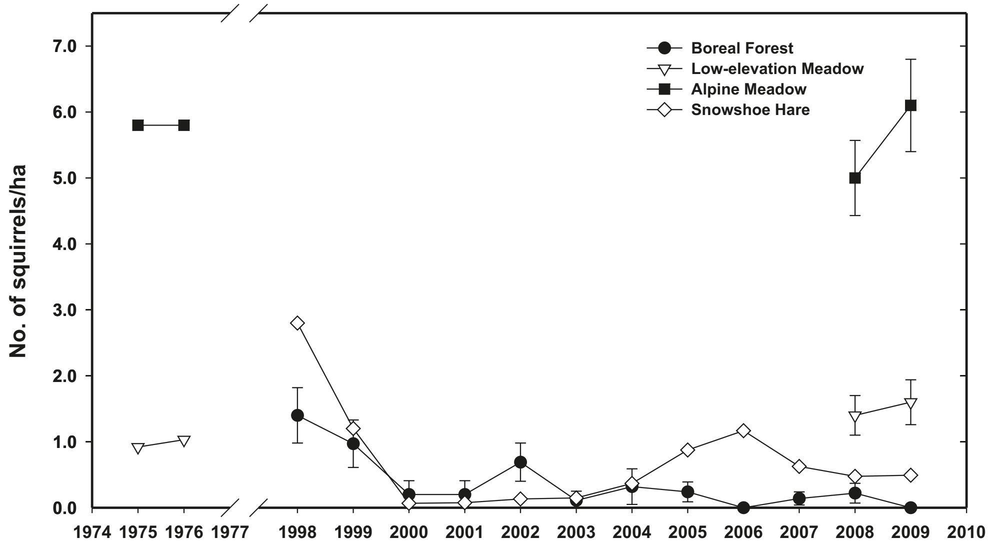
Density

Population density 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 to early August. Traps were set at 0800 at each permanent trapping location, checked every 1.5 h, and closed by 1230 each trapping day. All density estimates were calculated using the maximum likelihood (ML) spatial model within the program Density version 4.4 (Efford 2007; Efford et al. 2009) using all the default parameters. The ML spatially explicit capture–recapture model in the program Density version 4.4 was used because this model seems to provide reliable density estimates for small mammals (C.J. Krebs, personal communication, 2010)

Relative abundance

We indexed 18 populations of arctic ground squirrels throughout a 4000 km^2 area in the Kluane Region. Populations were indexed in boreal-forest, low-elevation-meadow, and alpine-meadow habitats 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 5 cm × 7 cm tiles were placed in all known burrows in a specified area and left for 6 h. 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 showed 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, Olathe, Kansas, USA; http://www8.garmin.com/, accessed 28 May 2011) 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 calculation of burrow density and the number of tiles retrieved was used to determine the density of active burrows. 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 activity of arctic ground squirrels is influenced by both time of day and weather, all indexing was

Fig. 2. Annual density estimates from livetrapping of arctic ground squirrels (*Urocitellus parryii plesius*) in three different habitat types in the Kluane region, Yukon Territory. Bars represent 1 SE. Sources: 1975–1976 data from Green (1977), and boreal-forest data and densitites of snowshoe hares (*Lepus americanus*) from Krebs et al. (2010).



carried out between 0800 and 1600 each day and during clear weather conditions.

Statistical analyses

All data are reported as means ± SE. All statistical analyses were calculated using the program JMP version 4.0 (SAS institute Inc., Cary, North Carolina, USA). Averaged densities of arctic ground squirrels, number of burrows/ha, and number of 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 a square-root transformation was applied to the relative abundance data to meet the assumptions of normality and equal variance.

Results

Density

Annual late summer densities of arctic ground squirrels along with concurrent densities of snowshoe hares are shown in Fig. 2. When averaged over all years, late-summer densities of arctic ground squirrels differed significantly between all habitat types ($F_{[2,19]} = 11.92$, $P < 0.001$) (Fig. 3). Densities were lowest in the boreal-forest (0.38 ± 0.13 squirrel/ha), higher in low-elevation-meadow (1.25 ± 0.22 squirrel/ha), and highest in alpine-meadow habitat (5.7 ± 0.22 squirrels/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 after the low cycle of snowshoe hares in 2002 and arctic ground squirrels did not increase in density during the subsequent increase phase of the cycle of snowshoe hares from 2002 to 2006. Arctic ground squirrels were essentially extirpated from this habitat type by 2007. However, densities in nearby low-elevation-meadow habitat within the boreal-forest zone remained stable during this same time (1.4 ± 0.3 squirrel/ha in 2008 and 1.6 ± 0.34 squirrel/ha in 2009). Densities in alpine-meadow habitat were four times as high (5.0 ± 0.57 squirrels/ha in 2008 and 6.1 ± 0.7 squirrels/ha in 2009).

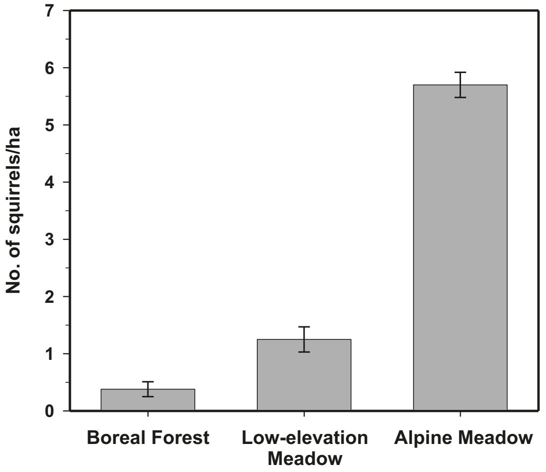
Relative abundance

A total of 18 populations were indexed throughout the Kluane region (5 boreal-forest habitats, 6 low-elevation-meadow habitats, and 7 alpine-meadow habitats). We found that the regional densities showed a similar pattern to our intensively livetrapped areas. The number of active burrows/ha increased from 0.1 ± 0.05 in the boreal forest to 64.0 ± 5.3 in low-elevation meadows to 332.3 ± 85.0 in alpine meadows ($F_{[2,17]} = 13.21$, $P < 0.0001$) (Fig. 4). The total number of burrows/ha, however, did not differ between boreal-forest (196 ± 9.0) and low-elevation-meadow (225 ± 9.0) habitats, but alpine-meadow habitat contained a considerably higher density of burrows (681 ± 8.0) ($F_{[2,17]} = 7.85$, $P < 0.01$) (Fig. 4).

Discussion

Both the mark–recapture density data and the regional population index data show that the density and relative abundance of arctic ground squirrels was lowest in the boreal forest, higher in nearby low-elevation meadows, and highest in alpine meadows. In 2006, populations of arctic ground squirrels in the boreal forests around Kluane Lake were completely extirpated. This habitat was subsequently recolonized by three individuals in 2007. This population went extinct again in 2009 (Fig. 2). In contrast, densities measured concurrently in nearby low-elevation-meadow and alpine-meadow habitats in 2008 and 2009 were significantly greater than those in the boreal forest and were very similar to those reported by Green (1977) (Fig. 2), who also studied arctic ground squirrels during the low phase of cycle of snowshoe hares. The regional abundance data (Fig. 4) also displayed a similar pattern to that of the measured density with the relative abundance of arctic ground squirrels increasing significantly from boreal-forest to low-elevation-meadow to alpine-

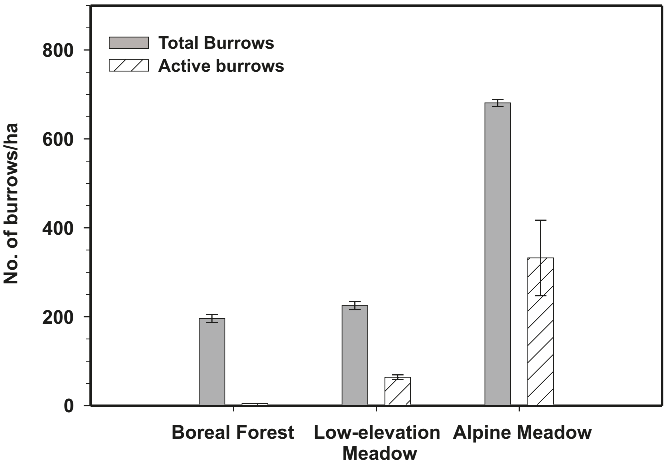
Fig. 3. Mean densities of arctic ground squirrels (*Urocitellus parryii plesius*) in the Kluane region, estimated by mark–recapture. Bars represent 1 SE. Boreal forest: *n* = 12 (1998–2009); low-elevation meadows: *n* = 4 (1975, 1976, 2008, 2009); alpine meadows: *n* = 4 (1975, 1976, 2008, 2009). Sources: 1975–1976 data from Green (1977) and boreal-forest data from Krebs et al. (2010).



meadow habitats. The population collapse of arctic ground squirrels in the boreal forest was a regional event and not a local event.

The ecological factors driving these density differences among habitats may include predation, food limitation, burrow limitation, disease, and climatic changes. Top-down limitation is likely an important factor continuing to limit populations of arctic ground squirrels in the boreal forest. For example, populations of arctic ground squirrels in the boreal forest typically exhibit cyclical fluctuations that are positively correlated with the 8–10 year cycle of snowshoe hares, but with a lag of 1–2 years (Boutin et al. 1995; Krebs et al. 2001). This lag is due to prey switching (Hubbs and Boonstra 1997). The increase phase of the cycle of snowshoe hares relieves predation pressure on arctic ground squirrels, which is a secondary prey species in the boreal forest. Population sizes of arctic ground squirrels in the boreal forest started to decline in 1998 at the same time as the cyclic decline in abundance of snowshoe hares. Arctic ground squirrels have remained low in the boreal forest from 2000 to the present, except for a slight recovery in 2002. Densities of snowshoe hares in the boreal forest began to increase again in 2004 with peak densities occurring in 2006; however, these peaks were less than half of those observed during the previous peak in 1998 (1.2 hares/ha in the 2006 peak vs. 2.7 hares/ha in 1998 peak; Sheriff et al. 2009). Numerous studies on arctic ground squirrels in the boreal forest have shown predation to be a major limiting factor particularly during times when densities of snowshoe hares 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 of arctic ground squirrels to recover in the boreal forest is probably affected by the relatively low densities of snowshoe hares since 2007. Studies comparing survival rates in boreal-forest, low-elevation-meadow, and alpine-meadow habitats are required to determine the importance of predation in limiting populations of arctic ground squirrels in the boreal forest.

Fig. 4. Relative abundance of arctic ground squirrels (*Urocitellus parryii plesius*) in different habitat types from 2008 to 2010 in the Kluane region, measured by burrow counts. Bars represent 1 SE. Boreal forest: *n* = 5; low-elevation meadows: *n* = 6; alpine meadows: *n* = 7.



Although the importance of food limitation in regulating herbivore populations has been disputed, it is possible that joint interactions between resource limitation and predation are inhibiting the recovery of populations of arctic ground squirrels in the boreal forest. In food addition and mammalian predator exclusion experiments at Kluane, densities of arctic ground squirrels 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, but this hypothesis needs to be explored by examining growth rates and body condition of arctic ground squirrels in different habitat types.

Burrows do not limit populations of arctic ground squirrels in the Kluane region. The similar number of burrows in boreal-forest and low-elevation-meadow habitats (196 ± 9.0 and 225 ± 9.0 burrows/ha, respectively) suggests that the availability of burrows is not a limiting factor in the boreal forest. The observed density differences between boreal-forest, low-elevation-meadow, and alpine-meadow habitats and the negligible difference in the total number of burrows per hectare between the boreal forest and low-elevation meadows suggests that burrow availability is similar and that another process is driving the observed density differences. Although burrow availability can be a significant limiting factor for populations in some alpine meadows and arctic tundra (Carl 1971; Batzli and Sobaski 1980), the majority of studies investigating populations of arctic ground squirrels in the boreal and sub-boreal have not shown 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 livetrapping of arctic ground squirrels in previous studies in the Kluane region, we saw no obvious indications of disease. Given the close proximity of boreal-forest populations to those in nearby low-elevation-meadow habitats, a disease present in the boreal forest would probably manifest itself also in low-elevation-meadow populations, something that was not observed during this study. Although there is some evidence for the ability of disease to limit populations of arctic ground squirrels (see Smith and Johnson 1985 and Cully and Williams 2001), there has been no indication of the presence of disease or disease outbreaks in populations of arctic ground squirrels in the Yukon boreal forest.

Climatic changes are expected to be the most pronounced in the polar regions and these changes may have the capacity to alter population dynamics of arctic ground squirrels both directly and indirectly. Direct effects include the increasing occurrence of winter rain events. These may affect hibernating arctic ground squirrels in two important ways: (1) reducing snowpack and (2) 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 and 2007, there were no major winter rain events observed during this study from 2008 to 2010. Since arctic ground squirrels produce yearly litter sizes ranging from 2 to 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-elevation 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 cycle of snowshoe hares. Since populations in the boreal forest have historically been correlated with changes in the 9–10 year cycle of snowshoe hares, 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 cycle of snowshoe hares 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 population dynamics of arctic ground squirrels.

The persistence of arctic ground squirrels in low- and high-elevation-meadow habitats and the concurrent extirpation of arctic ground squirrels from areas in the boreal forest provide preliminary evidence for the existence of the source–sink model rather than the balanced dispersal model. In the balanced dispersal model, the eventual equalized fitness of different habitat types should inhibit the possibility of populations in different habitat types being extirpated. In this study, we observed two instances (2006 and 2009) where arctic ground squirrels were extirpated from boreal-forest habitat types. It is possible that low-elevation-meadow habitats and alpine-meadow habitats display characteristics more indicative of the balanced dispersal model. These preliminary data are suggestive that the boreal-forest habitat is functioning as a population sink and that populations in nearby meadow habitats are potential populations sources; however, more detailed demographic data are required to explore this possibility. Although density data alone are often insufficient to assess habitat quality (Van Horne 1983), 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 we show that density and abundance of arctic ground squirrels vary 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 arctic ground squirrels in the southwest Yukon based on data collected in boreal-forest habitat would be inadequate in the absence of data collected in low-elevation-meadow or alpine-meadow habitat. The mechanisms underlying the large variation in density in boreal-forest, low-elevation-meadow, and alpine-meadow habitats need to be further explored, and future research should focus on the demographic processes responsible for these habitat differences.

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