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Evidence for source–sink dynamics in a regional population of arctic ground squirrels (*Urocitellus parryii plesius*)

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Abstract

Context. 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.

Aims. Arctic ground squirrels (*Urocitellus parryii pleisus* (Osgood, 1900)) occupy a large geographic area in northern Canada and live in a variety of habitat types, including boreal forest, low-elevation meadows and alpine meadows, providing an opportunity to investigate the possible existence of source–sink dynamics.

Methods. We hypothesised that arctic ground squirrels in the south-western Yukon exhibit demographic characteristics indicative of source–sink dynamics. Boreal forest habitat could be a sink in spite of previous high squirrel densities, whereas meadows could be a source. We investigated this by mark–recapture live-trapping and radio-telemetry.

Key Results. In the boreal forest in the Kluane region, we found reduced recruitment, reduced population growth rates (λ), and reduced survivorship for radio-collared individuals that moved from low-elevation meadows into the boreal forest. There was no evidence from radio-collared juveniles of dispersal from high-density ground squirrel populations in alpine meadows down into boreal forest.

Conclusions. Boreal forest is a sink habitat for arctic ground squirrels. Source–sink dynamics observed between low-elevation meadow and boreal forest habitats appear to result from increased predation pressure in the boreal forest. The result has been a near extirpation of boreal forest arctic ground squirrels in the Kluane region since 1998.

Implications. Because the source areas of low-elevation meadows occupy only 7–9% of the lowland habitat, recolonisation of boreal forest sites has been very slow. Whereas alpine populations remain high in 2011, boreal forest populations remain near zero. Alpine populations do not appear to be a source for the boreal forest.

Additional keywords: habitat-specific demography, Yukon *Urocitellus parryii plesius*.

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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 that describes a species occupying at least two different habitat types, sources and sinks (Pulliam 1988; Leibold *et al*. 2004). In source habitats, reproduction exceeds mortality and a surplus of dispersers is produced. Conversely, in sink habitats 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. It has provided valuable insight into the mechanisms underlying species residency in unsuitable habitat types.

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 effective conservation efforts (Brawn and Robinson 1996; Kristan 2003; Perlut *et al*. 2008; Kanda *et al*. 2009). For example, identifying source–sink dynamics has been important for prioritising contemporary conservation actions designed to protect high-quality source rather than sink habitat for rare and threatened species (Lampila *et al*. 2009; Nappi and Drapeau 2009; Schooley and Branch 2009). 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.

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 are often inadequate to differentiate between sources and sinks because 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 animal 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, namely, 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 be positively correlated with the 10-year snowshoe hare (*Lepus americanus*) 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 (Gillis *et al*. 2005; Donker and Krebs 2011). Conversely, populations in alpine meadows are 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. The present study is the first to compare arctic ground squirrel demographic rates in three different habitat types, including boreal forest, low-elevation meadow and alpine meadow.

Here, we compare three habitat types (boreal forest, low-elevation 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, we 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 characterised by two distinct habitat units, namely, meadow (source) and boreal forest (sink), that display discrete demographic rates independent of those at higher elevations.

Materials and methods

Study species

Arctic ground squirrels occupy arctic tundra, alpine areas and the boreal forest of north-western Canada and Alaska (Nadler and Hoffman 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 on emergence in spring and produce one litter per year ~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 three different habitat types at five locations in the Kluane Region, Yukon Territory (Fig. 1). 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 by us at two 10-ha study sites (~900 m asl; 61°00′38″N, 138°11′31″W and 60°55′53″N, 137°58′25″W) located ~20 km from each other. These two boreal forest sites were the same ones as used in a previous study by 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 (60°59′56″N, 138°33′31″W) and had been used previously by Green (1977). The first 12-ha alpine-meadow study area (~1800 m asl) (61°12′50.2″N, 138°16′39.9″W) 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 (the site used by Gillis *et al*. 2005). The second alpine-meadow study area (10 ha, ~1600 m asl) was located in KNPR and ~8 km uphill from the low-elevation meadow site in south-facing alpine-meadow habitat (61°01′06″N, 138°37′34″W), was previously used by Green (1977) and was reutilised by us. Previous data for ground squirrels in the boreal forest were compiled from Boonstra *et al*. (2001), Gillis *et al*. (2005) and C. J. Krebs (unpubl. data). Data for low elevation meadow and alpine-meadow habitat for 1975–1976 were obtained from Green (1977). Data for the first alpine-meadow study area was obtained from Gillis *et al*. (2005).

All study areas lay within the rain shadow of the St Elias Mountains and, therefore, the climate is characterised by cool, dry weather conditions (total annual precipitation ~280 mm, average annual temperature –3.8°C (Environment Canada, Canadian Climate Normals, http://climate.weatheroffice.gc.ca/climate_normals/index_e.html).

Trapping and handling

Squirrels were trapped using Tomahawk live traps (14 × 14 × 40 cm, Tomahawk live trap Co., Tomahawk, WI, USA) baited with peanut butter. In the boreal forest, arctic ground squirrels were trapped on two 10-ha grids, with 50 traps spaced 30 m apart in a 10 × 10 array, with traps placed at alternate grid stakes (e.g. A1, B2, A3). At the low-elevation meadow site, squirrels were trapped on a 9-ha grid, with 50 traps spaced 50 m apart in a 5 × 10 array, with a trap at each grid stake. At the first alpine-meadow site, squirrels were trapped on a 12-ha grid, with 49 traps spaced 50 m apart in a 7 × 7 array, with a trap at each grid stake. At the alpine-meadow site in KNPR, trapping occurred on a 9-ha grid, with 49 traps placed

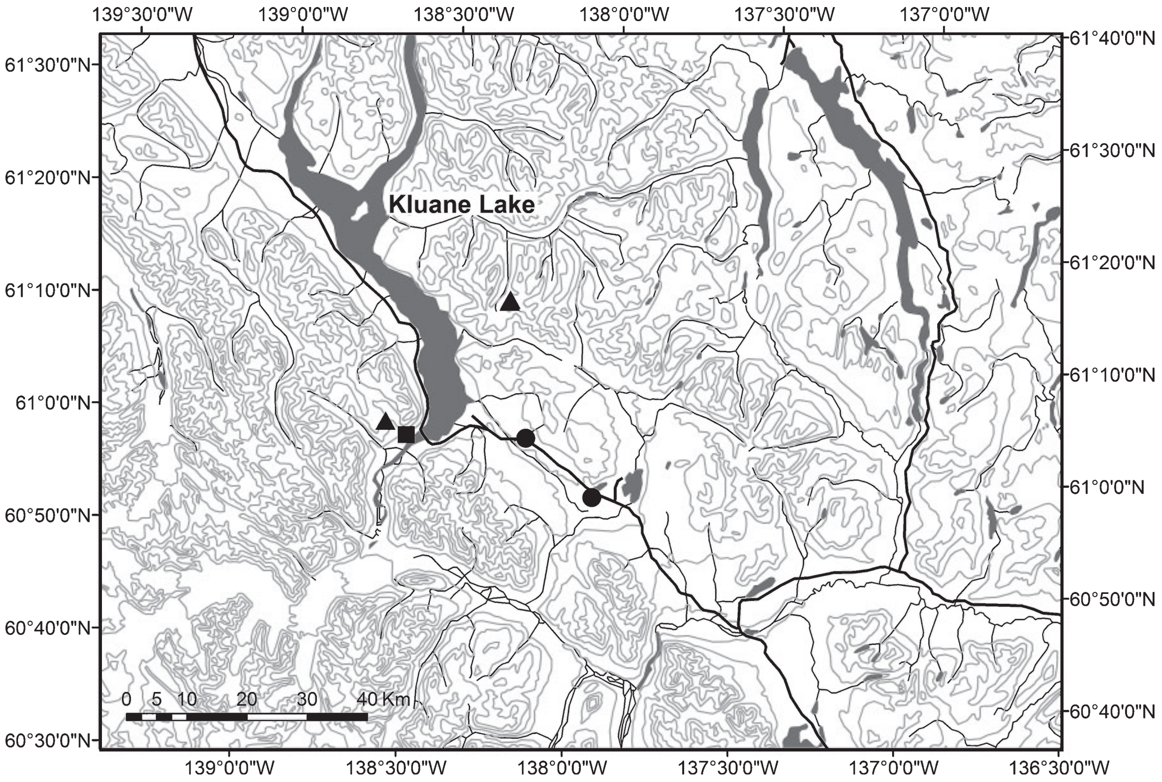

Fig. 1. Location of the study area in the south-western Yukon, Canada. Circles represent boreal forest trapping grids, the square represents the low elevation-meadow trapping grid and triangles represent alpine-meadow grids.

50 m apart in a 7 × 7 array, with a trap at each grid stake. Trappability of arctic ground squirrels is very high (77% adults, 88% juveniles, Hubbs and Boonstra 1997) and trapping sessions continued on each site for 2–6 days (mornings only) until very few new animals were caught. Trapping effort was somewhat variable in the different studies summarised here, but the end goal for every trapping session for every study was to capture the entire ground squirrel population on the trapping grid.

After capture, all ground squirrels were transferred to a mesh bag, tagged with monel No. 1005-1 tags (National Band and Tag Co., Newport, KY, USA) in both ears, weighed with a Pesola spring scale (±5 g), sexed and measurements of skull width (±0.5 mm) were taken. This research protocol was approved by the University of British Columbia Animal Care Committee, in accordance with the guidelines of the Canadian Council for Animal Care.

Adult survival

Adult female arctic ground squirrel survival was divided into active-season survival and over-winter survival. Active-season survival was calculated as the proportion of adult 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 adult females caught in the fall trapping session that were re-caught following spring. Only female ground squirrels were used in the survival analysis because they do not disperse. These survival estimates were based on direct enumeration because arctic ground squirrels are highly trappable and our data represent a complete census of each study area.

Juvenile survival and dispersal

Radio-telemetry was used to calculate active-season survival and dispersal distances for juvenile arctic ground squirrels in both study areas in KNPR during the 2009 active season. In total, 34 juvenile arctic ground squirrels (17 from low elevation-meadow site, 17 from alpine-meadow site) were fitted with expandable 5-g radio-collars (PD-2C transmitters, Holohil Systems Limited, Carp, Ontario, Canada). Sample sizes were constrained by our research budget. 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. Dispersal distances were determined using a handheld GPS unit (Garmin GPSmap60cx, Olathe, KS, USA) and measured as the straight-line distance from the location of capture at emergence to late August when juveniles had 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 three 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 three locations was used.

Recruitment and population growth rate (λ)

To compare recruitment among habitat types, 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 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 were used and data were pooled for both sexes. For all models, survival (φ) and λ were modelled as time-dependant, whereas recapture probability (*P*) was time constrained. Because time constraints on values of φ and λ generally do not make biological sense and fully time-dependant models result in the first and last λ values being inestimable (Franklin 2001), constraints were placed only on recapture probabilities (which were very high). For further details of Pradel models in program MARK, see Franklin (2001).

Statistical analyses

All data are given as means ± s.e. All statistical analyses were calculated using program JMP v4.0 (SAS institute, Cary, NC, USA). Active-season survival, over-winter survival and the ratio of juveniles to adults were analysed using a one-way ANOVA with Tukey's *post hoc* tests. Sample sizes for these calculations are given in Table 1. Prior to analysis, all data were assessed for normality and homogeneity of variance and either transformed or analysed 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 analysed 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).

Results

Adult survival

Female arctic ground squirrels in the boreal forest survived poorly (43% ± 5 per 4 months, $n = 18$ years) over the 4-month active season, compared with female arctic ground squirrels in both low-elevation meadow (73% ± 10, $n = 4$ years) and alpine-meadow habitats (80% ± 8, $n = 7$ years) ($F_{2,28}$, $P = 0.001$) (Fig. 2). No significant differences were observed in over-winter survival between habitat types ($F_{2,26}$, $P = 0.23$), although there is a suggestion that female arctic ground squirrels might survive better over winter in boreal forest (65% ± 5 per 8 months, $n = 16$ years) and low elevation-meadow (66% ± 9, $n = 4$ years) habitats than in alpine habitats (51% ± 8, $n = 6$ years).

Juvenile survival and dispersal

In total, 34 juveniles were radio-collared in the summer of 2009. Kaplan–Meier 38-day survival estimates were calculated only for males because they are the dispersing sex (Fig. 3). Overall, survival of female juveniles was similar to that of male juveniles in this small sample. The pattern of survival is particularly clear. Late-summer male-juvenile survival is good in alpine habitats (90%) and poor in low-elevation meadows (40%). Radio-collared juveniles in low elevation-meadow habitat also moved farther (Fig. 4) than those in alpine-meadow habitat (low meadow 319 m ± 71 *v.* alpine meadow 76 m ± 71). Eleven juveniles (8 males, 3 females) of the 17 collared in the low elevation-meadow habitat moved to boreal forest habitat, and 8 (73%) of these 11 were subsequently killed by predators in the forest. We used the kill key developed by the Kluane Project (Krebs *et al*. 2001) to determine that predation by either northern goshawk (*Accipiter gentillis* (L. 1758)) or red-tailed hawk (*Buteo jamaicensis* (Gmelin, 1788)) accounted for 100% of the radio-collared ground squirrel mortalities in the boreal forest. All six individuals (3 males, 3 females) that remained in meadow habitat survived the entire 38-day period from 12 July to 19 August. No movements between low elevation-meadow habitat and alpine-meadow habitat were observed.

Recruitment and population growth rate (λ)

Boreal forest habitat contained a significantly lower juvenile to adult ratio (0.44 ± 0.18, $n = 9$ years) than both low elevation-meadow (1.14 ± 0.11, $n = 4$ years) and alpine-meadow (1.41 ± 0.26, $n = 10$ years) habitat types ($F_{2,22}$, $P = 0.01$) (Fig. 5). Estimates of λ from fall to fall were 0.68 ± 0.2 for boreal forest ($n = 9$ years), 0.90 ± 0.21 for low elevation-meadow ($n = 1$ year) and 0.98 ± 0.13 for alpine-meadow ($n = 1$ year) habitats respectively. These differences are not statistically significant and are at most indicative of a possible pattern that could be tested only with a much larger sample of concurrent years in all habitats. In particular in the boreal forest since 1998, populations of ground squirrels have been so low that population growth rates are based on so few animals that they are biologically unreliable. Population growth rates recorded by Green (1977) from 1975 to 1976 at the same

Table 1. Sample sizes for the survival, recruitment and population growth results

Parameter	Boreal forest 1992–2010		Low meadow 2008–09		Alpine meadow 2008–09		Alpine meadow – Gillis *et al*. (2005) data	
	No. of individuals	No. of years of data	No. of individuals	No. of years of data	No. of individuals	No. of years of data	No. of individuals	No. of years of data
Active-season survival	238^A	18	26^A	2	75^A	2	59^A	3
Over-winter survival	230^A	16	11^A	1	26^A	1	42^A	3
Recruitment	84^B	9	54^B	2	170^B	2	113^B	6
Population growth rate	84^B	9	54^B	1	170^B	1	–	–

[A] Adult females only.

[B] Juveniles and adults.

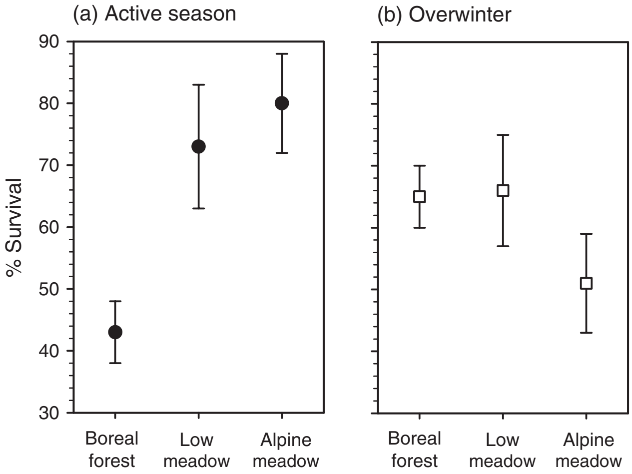

Fig. 2. Adult female arctic ground squirrel (*a*) active-season survival and (*b*) over-winter survival. Bars represent 1 s.e. Source of data: boreal forest, 9 years (C. J. Krebs, unpubl. data); low-elevation meadow, 4 years (2008–09 from the present study, and 1975–76 from Green 1977); and alpine meadow, 10 years (2008–09 from the present study, 1975–76 from Green (1977), and 2000–02 from Gillis *et al.* 2005).

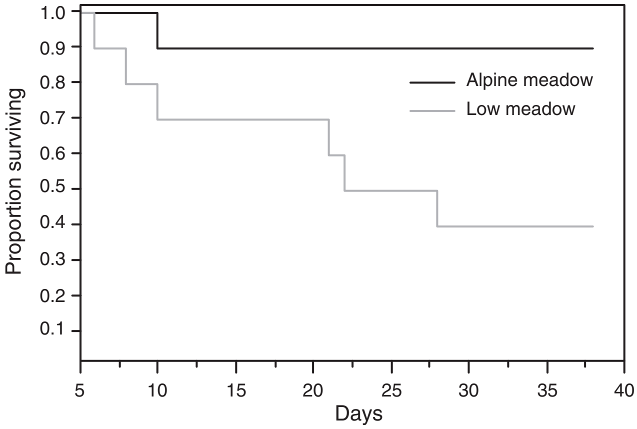

Fig. 3. Kaplan–Meier survival curves for radio-collared juvenile male arctic ground squirrels in late summer 2009. After 38 days, 40% survival in low-elevation meadow *v.* 90% survival in alpine medow; log-rank test; $\chi^2 = 5.16$, d.f. = 1, $P = 0.02$, $n = 20$.

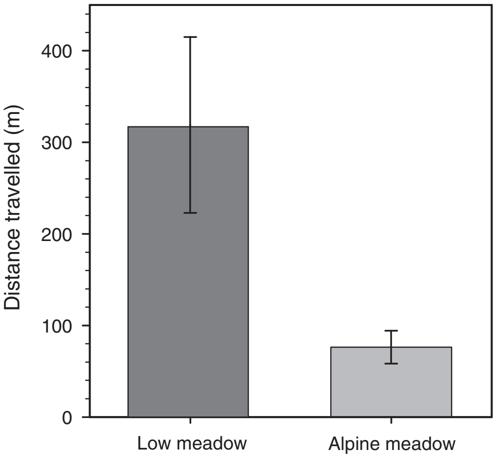

Fig. 4. Mean distance moved by radio-collared arctic ground squirrels in low elevation-meadow ($n = 15$) and alpine-meadow ($n = 12$) habitats in summer 2009. Bars represent 1 s.e.; Mann–Whitney *U* test, $\chi^2 = 10.40$, d.f. = 1, $n = 27$, $P = 0.001$.

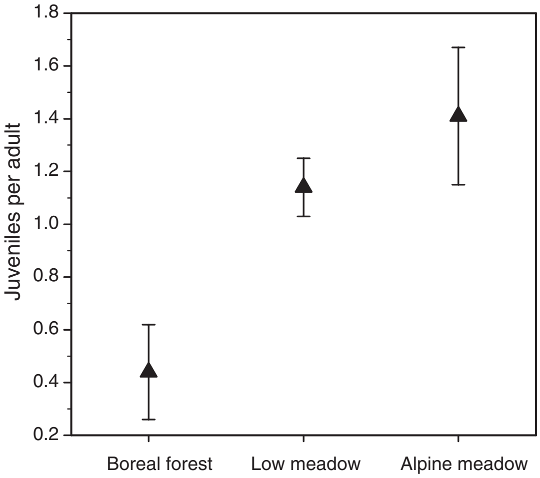

Fig. 5. Recruitment rate (juveniles per adult) of arctic ground squirrels in three habitat types. Bars represent 1 s.e. Sample sizes are given in Table 1. Source of data: boreal forest, 9 years (C. J. Krebs unpubl. data); low-elevation meadow, 4 years (2008–09 from the present study, and 1975–76 from Green 1977); and alpine meadow, 10 years (2008–09 from the present study, 1975–76 from Green (1977), and 2000–02 from Gillis *et al.* 2005).

low elevation-meadow and alpine-meadow study areas were 1.1 and 1.0 respectively.

Discussion

Our results rest heavily on the assumption of the uniformity of arctic ground squirrel demography over the past 18 years. If we can make that assumption, we can compare the extensive dataset previously obtained by Byrom *et al.* (2000), Karels *et al.* (2000) and Gillis *et al.* (2005) to the measurements obtained from the sites mapped in Fig. 1 for the 2008–10 period. We have shown in a previous paper (Donker and Krebs 2011) that there has been a change in the demography of arctic ground squirrels in the boreal forest habitats of the Kluane region since 1998. From 1976 (when our Kluane studies began) until 1998, arctic ground squirrels in the boreal forest followed the snowshoe hare cycle, increasing when hares increased and collapsing to low numbers when predators turned from the declining hare population to ground squirrels as alternative prey (Boutin *et al.* 1995; Boonstra *et al.* 2001). Throughout this period from 1976 to 1998, we assumed that boreal forest ground squirrels were self-replacing as a temporally fluctuating series of source years and sink years, largely as a consequence of predation associated with the snowshoe hare cycle. But since 1998, ground squirrel populations in the boreal forest collapsed to virtually zero and there has been almost no recovery by 2011. Forest sites, which in the past produced dozens of captures before 1998, have produced nearly zero since that time. In this situation, immigrants were essential to recovering the forest populations, and immigrants could come only from alpine meadows or from low-elevation meadows. Gillis *et al*. (2005) suggested that alpine meadows were not a source for boreal-forest squirrel populations, and if this is correct, the only possible source areas are low-elevation meadows. The dynamics of ground squirrels in the boreal forest since 1998 are then explicable by a collapse of the forest populations, coupled with a very limited source–sink dynamic between low-elevation meadows and forest habitats. It is this explanation that we have tried to test in the current research.

Our results reject the first hypothesis that arctic ground squirrels in alpine-meadow habitats function as population sources for low-elevation habitats and support the second hypothesis that low-elevation meadows are population sources and the boreal forest in the Kluane region is a long-term population sink. Surprisingly, the demography of populations in low-elevation meadows was more similar to that in alpine meadows than that in nearby boreal forest habitat that forms the matrix around these low-elevation meadows. Arctic ground squirrel populations in the boreal forest are smaller (Donker and Krebs 2011) and appear to exhibit demographic characteristics indicative of sink habitat types. The extirpation of ground squirrels from the boreal forest (Gillis *et al*. 2005; Donker and Krebs 2011), 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 a sink habitat for arctic ground squirrels.

Conversely, arctic ground squirrel populations in nearby low elevation-meadow habitat appear to be stable and self-sustaining and appear to function as sources for populations in the boreal forest. Juveniles in the present 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 Gillis *et al*.'s (2005) suggestion that boreal forest populations are functioning as population sinks and that nearby meadow habitats may provide the immigrants required to sustain arctic ground squirrel populations in the forest.

Alpine-meadow habitats support higher densities of arctic ground squirrels, which exhibit higher active-season survival rates than, and survive poorly over winter compared with, arctic ground squirrels in low-elevation habitats. Our animal-movement data provide no support for the hypothesis that alpine-meadow populations supplement low-elevation populations in a source–sink relationship. 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. In our study area, alpine ground squirrels would have to move 7 km downhill to reach the nearest boreal forest habitat.

Adult survival

The survival data suggest 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 with survival in low-elevation meadows, the movement of radio-collared juveniles from low elevation-meadow habitat into nearby boreal forest habitat and the subsequent high incidence of predation in the forest, 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 to be due to several factors, including a reduced ability to detect and avoid predators in boreal forest habitat, a higher abundance of predators, lack of alternative prey, and the small ground squirrel population sizes themselves in this habitat type. We suggest that boreal forest ground squirrel populations have fallen into a predator pit since 1998 and are yet to emerge from it in 2011.

Arctic ground squirrels live in a network of social groups located in close proximity that consist of various females and usually one territorial male. Specialised 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 are likely to be able to detect predators from further away and notify other members in the population sooner than are individuals in the boreal forest. The enhanced ability of arctic ground squirrels in low-elevation meadows to detect predators is likely to facilitate the persistence of low elevation-meadow populations when compared with squirrels in the boreal forest. The importance of group-vigilance behaviour 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 larger populations living in meadows, thus increasing their probability of extirpation in the forest habitat.

Juvenile survival and dispersal

During the present 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 of predation, does, however, provide evidence for the hypothesis that low-elevation habitat may be characterised by two discrete units, sources (low-elevation meadows) and sinks (boreal forest). Because adult females move very little (Karels and Boonstra 2000), the successful colonisation of boreal forest is hinged on 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 colonisation by juvenile arctic ground squirrel dispersing from low elevation-meadow habitats is likely to increase, thereby facilitating the re-establishment of boreal-forest populations. We were not able to study any potential movements of juveniles from boreal forest habitat to low-elevation meadows because there were no animals available to study in the boreal forest plots.

Recruitment and population growth rate (λ)

The low recruitment rates observed in the boreal forest compared with those in low elevation-meadow and alpine-meadow habitats suggest that arctic ground squirrel populations in the boreal forest are having smaller litter sizes and have lower juvenile survival after they leave the burrow. Unfortunately, determining litter sizes and reproductive success for individual arctic ground squirrel females is difficult because females are known to share natal dens (Lacey 1991). However, data from the present study show that juvenile active-season survival in boreal forest habitat is lower than that in low elevation-meadow and alpine-meadow habitats due to predation, and that individuals moving from low-elevation meadow into the boreal forest are at high risk of predation. 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 the present study provide further support that this habitat is functioning as a population sink.

Population growth rates observed here also tend to support the hypothesis that the boreal forest is functioning as a sink-habitat type. Data collected over a 10-year period during all phases of the snowshoe hare cycle show that population growth rates (λ) in the boreal forest rarely exceed 1.0, with an average value of 0.68 (Gillis *et al*. 2005). Although the λ-values presented here for both low elevation-meadow and alpine-meadow habitat were calculated in Program MARK for only a 1-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 as used in the present study, population growth rates of 1.0 (low-elevation meadow) and >1.0 (alpine meadow) are obtained. The persistence of arctic ground squirrels in the low elevation-meadow and alpine-meadow habitats in 2008–10, and the simultaneous extirpation of ground squirrels from the boreal forest since 1998 (Donker and Krebs 2011), provides supportive evidence that the boreal forest is functioning as sink habitat for arctic ground squirrels.

The onset of the increase phase of the snowshoe hare cycle expected by 2012 is expected to relieve predation pressure in low-elevation ground squirrel habitat and allow arctic ground squirrel populations to re-establish themselves in the boreal forest via dispersal from nearby meadow habitat, as we observed in the present study. Given that open meadow habitat comprises only 7–9% of this study area (Krebs *et al*. 2001), the recolonisation of extirpated ground squirrel populations in the boreal forest may take a considerable amount of time. The present study has provided empirical support for source–sink population dynamics in a wildlife population. It has provided a cautionary tale for conservation programs attempting to revive a source–sink situation in which the source areas are very small relative to the sink area.

Future research should focus on the genetic relatedness of arctic ground squirrels in low elevation-meadow, alpine-meadow and boreal forest habitats to further determine the level of connectivity among these habitats (O'Keefe *et al*. 2009). A similar study when the densities of snowshoe hare are high will also help clarify whether the sink characteristics observed in the boreal forest are permanent or vary temporally. Experimental tests for source–sink dynamics could involve the isolation of arctic ground squirrels in both low elevation-meadow habitat and boreal forest habitat and subsequent monitoring of population persistence.

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