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Factors Governing the Distribution and Abundance of Arctic Ground Squirrels

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INTRODUCTION

Extinction is the most extreme future state for any wildlife population. In Canada's northern montane boreal regions, the disappearance of any small herbivore will have consequences for the way energy flows between trophic levels. Arctic ground squirrels (*Urocitellus parryii plesius*) were once so plentiful as to be responsible for approximately one-quarter of the energy flow at the herbivore level (Boonstra et al., 2001). However, population dynamics of this species over the past decade serve as a potent example of how northern regions may now be in dramatic flux.

The Arctic ground squirrel is the largest ground squirrel in North America and has the most northerly distribution (Fig. 1). It lives throughout the montane boreal, alpine, and tundra regions and hibernates from September to mid-April (Naughton, 2012). In the Yukon, it is an important seasonal food source for many predators, including lynx (*Lynx canadensis*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), wolf (*Canis lupus*), black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), wolverine (*Gulo gulo*), Red-tailed Hawk (*Buteo jamaicensis*), Northern Goshawk (*Accipiter gentilis*), and Golden Eagle (*Aquila chrysaetos*). Arctic ground squirrels are also hunted by Yukon First Nations as a traditional source of food. Population fluctuations of Arctic ground squirrels therefore affect the food supply available to a wide list of predators.

FIG. 1. Adult female Arctic ground squirrel. (Photo: J. Werner.)

For almost three decades (1973–99), ground squirrel populations in the boreal forests of the Kluane region (SW Yukon) cycled in a predictable manner (Werner et al., 2015b) in concert with the snowshoe hare (*Lepus americanus*; Boutin et al., 1995). This 9–10 year cycle was stable up until 2000. In that year, populations crashed, and they have not, as yet, recovered. This once important species declined from 17% of the regional herbivore biomass to nearly zero. Most boreal forest populations (~95%) are now extinct, as are a large fraction (~65%) of nearby meadow populations. I am now conducting experiments and surveys designed to clarify the likely causes and consequences of these dramatic changes. The measures described below are intended to address a number of specific research projects.

RESEARCH QUESTIONS AND PRELIMINARY FINDINGS

The disappearance of a number of colonies in the Kluane area was initially documented by a long-term ecosystem monitoring program spanning more than 40 years (C. Krebs, pers. comm. 2014). Uncertainty regarding whether these parochial data sets reflect large regional patterns inspired me to conduct population surveys of 221 identified colonies over a 25 000 km^2 area of south-central Yukon (Fig. 2). Survey results indicate that, although extinctions are commonplace throughout the region, colony occupancy rates are habitat-specific. For example, alpine habitats are least affected by population collapses, as are open areas near or adjacent to active human infrastructure (e.g., highways, airports, fenced pasture). In contrast, most low-elevation meadow and forest colonies are now extinct. Many large populations that historically supported prolonged scientific study are completely gone (e.g., Green, 1977; McLean, 1985; Krebs et al., 2001; Lacey and Wieczorek, 2001).

When considering wildlife populations across heterogeneous habitats, it becomes necessary to address the role of habitat quality in determining dispersal rates between patches and the occupancy status of a patch at any given time (Pulliam, 1988). "Source" habitats are net exporters of individuals. In these high-quality habitats, natality exceeds mortality, and connectivity with other habitat patches facilitates successful dispersal. In poor-quality habitat, local yearly recruitment is not related to reproduction or survival rates of patch residents. These "sink" habitats are net importers, and without sufficient immigration from source habitats, extinction would be inevitable (Dias, 1996). Previous studies have identified forests as potential sink habitats that require a constant influx of squirrels from surrounding source habitats to sustain them (Gillis et al., 2005; Donker and Krebs, 2012). To better understand the consequences of this source-sink relationship, I compared body mass and condition of adult females in boreal forest and adjacent meadows using data accumulated between 2000 and 2013. Condition was measured as mean mass adjusted for structural size (residuals). Results indicate strong tendencies toward habitat-specific reproductive condition among females. During spring, forest squirrels weighed less (405 ± 7 vs. 437 ± 11 g; mean ± SE) and were in poorer body condition than meadow squirrels (Fig. 3; mean (± SE) residual of mass over structural size = −11.0 ± 10.2 vs. 20.5 ± 6.1 g; Werner et al., 2015a). Females that are in poor condition often exhibit lower reproductive success, a fact that has been reported for ground squirrels in the boreal forest (Gillis et al., 2005). However, I also found that forest squirrels gained mass at an accelerated rate, and by autumn, they had attained parity with squirrels in more favorable habitats (both groups weighed 520 ± 15 g; Werner et al., 2015a). I hypothesize that achieving compensatory mass gain likely comes at the cost of having to prioritize foraging over vigilance, thereby reducing active-season survival.

A large-scale attempt to identify causes of colony extinctions involved the use of landscape-level surveys across the southern Yukon (Fig. 2). These surveys measured colony characteristics considered to reflect levels of food availability (e.g., richness and abundance of food plants, soil composition) and predation risk (distance-specific visibilities, slope angle, distance to predator cover). To estimate population density, I used a powder tracking method developed by Boonstra et al. (1992) for lemmings and voles, but adapted for ground squirrels (Hubbs et al., 2000; Donker and Krebs, 2011; Werner et al., 2015b). Small (5 × 7 cm) black plastic tiles, covered in mineral oil and unscented talcum powder, were placed in all burrows within a specified area (minimum size 0.5 ha) and left for six hours. If the retrieved tile contained ground squirrel footprints, the burrow was considered active. Hubbs et al. (2000), who validated this method with mark-recapture data, report a strong linear relationship between active burrows per hectare and population density.

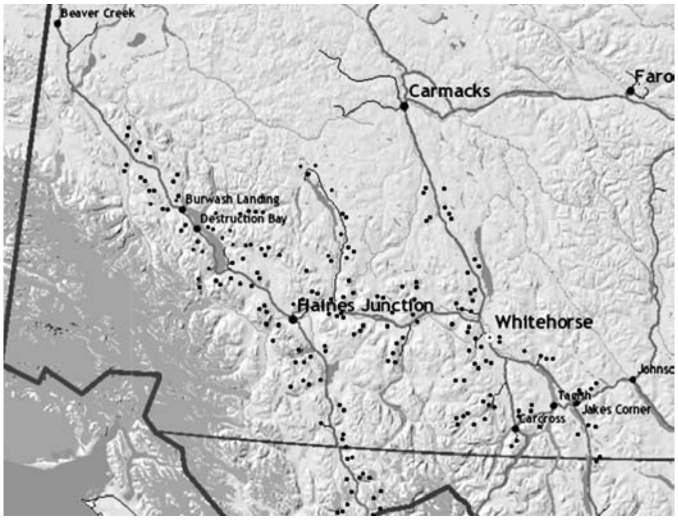

FIG. 2. Locations of population density estimates for Arctic ground squirrel colonies, southern Yukon, Canada.

I then fitted negative binomial regression models to the data to determine whether population density is most sensitive to bottom-up (food) or top-down (predator) processes. Although both food and predators likely operate simultaneously to limit populations (Hubbs and Boonstra, 1997), I focused on these two competing models because of their contrasting predictions of how ground squirrels will respond to future environmental change. For example, climatic warming may result in greater primary production that should benefit populations limited by food. On the other hand, milder winter temperatures may promote the northward expansion of generalist predators. Prey populations currently limited by predators are predicted to suffer under conditions of elevated predation pressure (Elmhagen et al., 2015). Results indicate that a model based on predation is more than 100 times as likely as a food-based model to predict population densities across the southern Yukon.

The notion that predation may now play a structuring role in the montane boreal system led me to analyze 23 years of ground squirrel mark-recapture density estimates for patterns consistent with predator limitation. I used multi-decadal spring and autumn census data (C. Krebs, unpubl. data) to calculate and plot instantaneous rates of population growth over population density. I also fitted regression relationships to annual ground squirrel and snowshoe hare densities. I found 1) evidence for a hyperbolic curve in the instantaneous rate of summer population change (May – September) of ground squirrels relative to their population density, 2) a single stable upper equilibrium around which numbers typically fluctuate, and 3) a lower critical density threshold below which populations drift to extinction. The crossing of this unstable boundary resulted in the subsequent uncoupling of ground squirrel and hare populations following their mutual decline phases in 1998. Such patterns are symptomatic of ground squirrel predators exerting a Type II functional response (Fig. 4; Sinclair and Krebs, 2002). This fact is significant because predators with

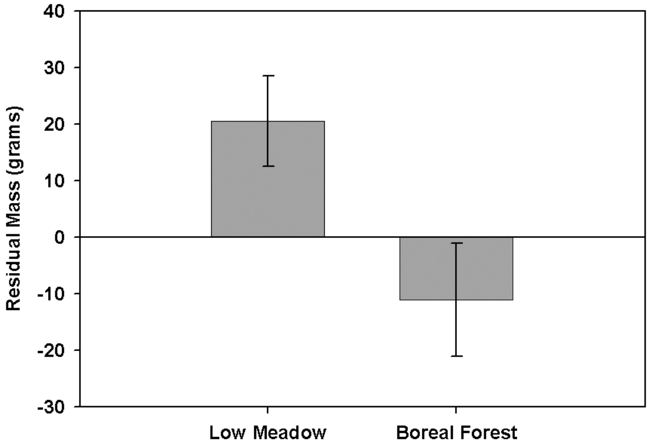

FIG. 3. The spring body condition index of adult female Arctic ground squirrels in two contrasting, low-elevation (~800 m) habitats (boreal forest and meadows) of the Kluane region, SW Yukon. Bars represent 1 SE. Data from Werner et al. (2015a).

Type II functional response are more likely to drive their prey to extinction. Inverse (i.e., negative) density dependence at low population size can also result from social dysfunction (Allee, 1931). Distinguishing between these two mechanisms would be difficult today because populations in the boreal forest are now largely extinct (Werner et al., 2015b). Note, however, that some extrinsic factor must first reduce populations to that critical threshold for these intrinsic Allee effects to take over.

Whether we are witnessing a permanent range contraction or a low phase to be followed by population recovery depends on whether the primary threatening processes have abated. My monitoring of large historical colony sites in Kluane (n = 14 colonies over six years, 2009 – 15) indicates that recolonizations are likely to be infrequent (none have been recorded to date). Therefore, during 2013 – 15 I experimentally reintroduced squirrels back into several large (~100 ha) historical meadow habitats. One of these meadows is situated on Kluane First Nation settlement land (61˚23′21.35″ N, 139˚6′13.86″ W) and historically supported a sustainable traditional harvest (G. Pope, pers. comm. 2012). My purpose is to understand if and why habitat quality has been reduced to the point at which such meadows can no longer support viable populations. A portion of these translocated squirrels were fitted with radio collars (Holohil pd-2C units; n = 105) so that I could monitor their habitat use, minimum daily movement distances, and active season survival. Source populations were taken from the Burwash Landing airport (61˚22′5.85″ N, 139˚1′43.10″ W).

As a means of increasing the strength of inferences to be drawn from this reintroduction project, one meadow was converted into a large (13 ha) choice experiment. I manipulated grass height and visibility (short grass and long grass treatments) and the number of available burrows. Treatment units were 50 × 50 m in size, oriented in a 5 × 10 pattern using a randomized block design. For the short grass treatment, vegetation height was reduced to 10 cm (range 0 – 23 cm) using gas-powered string trimmers. The tall grass treatment consisted of unmanipulated grassland with a mean height of 94 cm (range 15 – 114 cm). To alter burrow density, artificial burrows (50 cm deep and 7 cm in diameter) were dug using both gas- and hand-powered augers. The low-density treatment was set to 50 burrows per hectare (approximately the number of natural burrows found in situ) and the high density treatment was increased to 200 burrows per hectare.

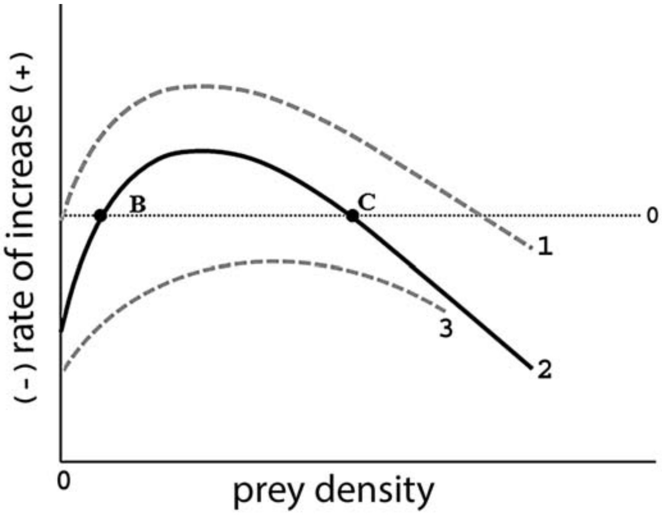

FIG. 4. An illustration of the instantaneous rate of change for a prey population experiencing varying levels of Type II predation. Point C represents a stable equilibrium most likely determined by food regulation. Point B is an unstable prey density threshold below which predators can cause extinction. Curves 1 and 3 represent different levels of predation intensity (1 = lowest; 3 = highest), while Curve 2 is believed to best approximate historical (2000 to the present) population dynamics of Arctic ground squirrels in the boreal forest region of Kluane, Yukon. Adapted from Sinclair and Krebs (2002).

These data are still being analyzed. However, several themes have already emerged. First, active season survival of translocated individuals was generally low (0% – 50%), and nearly all mortalities (> 90%) were due to predation by coyotes or Red-tailed Hawks. A major complicating factor is that reintroductions often fail because translocated animals exhibit low site fidelity (Armstrong and Seddon, 2008). My efforts were not unique in this respect: more than half of the ground squirrels moved out of the specified meadow and into surrounding forest. All of the dispersers from 2013 perished, prompting me in subsequent years to initiate soft release methods (e.g., the use of pre-release cages provisioned with food, water, and electric fencing; Fig. 5) as a means of promoting site fidelity (see Table 1 for specific reintroduction details). In general, only those squirrels that settled in or near the experimental treatments survived their first summer.

Second, the use of larger release group sizes during 2014 – 15 resulted in a corresponding shift from

TABLE 1. Description of reintroduction processes. Most individuals were telemetered and monitored every other day from 5 July through 10 August 2014.

Release type	Summary	Approximate number
Hard	Morning capture; immediate transport (~1 hour); release from cages at reintroduction site.	100
Firm	Morning capture; immediate transport as family groups (~1 hour); released into separate artificial burrows with supplemental food (apple, sunflower seeds); burrow entrance plugged temporarily (~2 hours); each individual was released into one of the treatment units, which contained either short (cut) or tall (natural) grass and either 200 (augmented) or 50 (natural) burrows per hectare.	100
Soft	Morning capture; immediate transport (~1 hour); housed in separate cages (1.8 × 1.2 × 0.75 m) for a two-week acclimatization period; cages were situated within the release meadow, arranged in a 5 × 5 pattern 20 m apart; water and food (rabbit chow, apple, natural forage) were provided for ad libitum consumption; all cages protected from large mammalian predators by a single five-strand electric fence.	25

FIG. 5. Jeff Werner setting up soft-release nest boxes and electric fencing at the Duke River meadow reintroduction site (Kluane First Nation settlement land). (Photo: J. Werner.)

reintroduction failure to success (~50% annual survival). This result is consistent with the extinction thresholds predicted by predator-prey theory (Sinclair et al., 1998) and with the patterns previously observed in the monitoring data. Minimum group-size effects can be the result of social facilitation (i.e., Allee effects), as has been recorded for other rodent species (e.g., Brashares et al., 2010). Future experiments will be necessary to disentangle what mechanisms are responsible for these group-size effects.

Third, during post-reintroduction monitoring, unmarked ground squirrels from unknown sources were observed moving to and settling in the reintroduction area. Regular monitoring of five nearby control plots (to monitor immigration) indicated that areas farther from the reintroduction site remained unoccupied despite the presence of adequate forage and burrow shelter. These findings point to the potential importance of patch occupancy and to the role that conspecific attraction (Smith and Peacock, 1990) may play in the settlement decisions of dispersing squirrels. In keeping with these observations, Weddell (1991) reported that marked Columbian ground squirrels (*Urocitellus columbianus*) visit many suitable empty patches but settle only in occupied areas. A strong reliance on the use of conspecific cues for targeting high-quality habitat will impede population expansion via the recolonization of extinct patches. During July and August 2015, I formally tested the conspecific attraction hypothesis, using camera traps to monitor caged females placed in vacant meadows. The data will be analyzed during 2016.

THE BIGGER PICTURE

This ongoing research has wider relevance because processes driving the altered population dynamics of Arctic ground squirrels are likely implicated in wider patterns of ecosystem change. Climatic warming of northern ecosystems is predicted to intensify the role of predation in regulating small herbivores (Legagneux et al., 2014). The mechanisms behind both top-down and bottom-up population control are sure to upset the trajectory of other medium body sized prey. If the loss of this herbivore from the boreal forest is not naturally reversed, predator pressure on other herbivores of the montane boreal zone is likely to change significantly. Local regimes of soil disturbance, nutrient cycling, and plant diversity are also expected to change as processes such as tunnel building, food caching, and selective foraging are lost.

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