ENVIRONMENTAL FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF RICHARDSON'S GROUND SQUIRRELS

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Ashley Nicole Fortney, candidate for the degree of Master of Science in Biology**,** has presented a thesis titled, ***Environmental Factors Affecting the Distribution and Abundance of Richardson's Ground Squirrels,*** in an oral examination held on September 24, 2013. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

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ABSTRACT

Richardson's ground squirrels (RGS) (*Urocitellus richardsonii*) are an important species for the grassland ecosystem on the Northern Great Plains of North America. They are a main source of prey and burrows for many prairie species including several Species at Risk (SAR) of extinction. RGS are also maligned as agricultural pests and managed extensively via poisoning. Control programs have negative consequences for RGS and non-target species, including some SAR. Despite their ecological importance and agricultural pest status, little is actually known about their distribution on the landscape and habitat variables that influence their distribution and abundance. This lack of knowledge is a major impediment to development of conservation strategies for SAR that are significantly impacted by the management of RGS, and a key limitation for forecasting conflicts with agricultural producers. The objective of my research was to provide information on the distribution of RGS and determine how habitat variables influence their presence and abundance.

I surveyed for the presence (detected at a site) and abundance (number of individuals) across a large area (130,000 km^2) of RGS range on the Canadian prairies during 2011 and 2012 using an alarm call-playback method. I found that RGS were not distributed evenly on the landscape. RGS were only detected at 157 (8%) of 1,900 systematic survey points across Saskatchewan, with an average of 3.3 ± 0.4 individuals per used location. In 2012, additional searches to locate larger colonies in the high-conflict (between RGS and agricultural producers) area of

southwestern Saskatchewan resulted in 31 colony locations with an average of 10.1 ± 1 RGS per colony. The systematic broad-scale surveys and more random colony searches revealed fewer and more patchily distributed RGS than expected given their pest status.

I used multivariate Resource Selection Function (RSF) modeling to examine RGS habitat selection. Habitat variables included in the analysis were vegetation height, land cover types, land use, and proximity to water, shrubs, trees, and buildings/structures. Vegetation height was the top predictor of RGS presence and abundance; vegetation height above 15-30 cm was associated with a drastic decrease in the probability of habitat use. RGS presence was positively influenced by the percentage cover of grass in an area and bare ground when greater than 10% of the land cover. The proximity to trees within 400 m had a negative effect on RGS presence, as did proximity to shrubs and water on RSG abundance. Lastly, RGS abundance was positively influenced by finely textured soils and tilled crops, while negatively affected by increasing percent shrub cover. My data on RGS distribution and habitat selection can be used to implement integrated pest management strategies, such as through the inclusion of habitat modification, and will also provide valuable information to aid conservation planning for SAR that rely on RGS.

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DEDICATION

To all my friends and family, especially my grandparents, my parents, and Steve.

Thank you for everything!

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1. INTRODUCTION

1.1 Richardson's Ground Squirrels: Natural History and Ecology

The Richardson's ground squirrel (RGS; *Urocitellus richardsonii*) is a North American species of ground dwelling squirrel. RGS were formerly classified in the genus *Spermophilus*, however, recent morphological and phylogenetic analyses prompted a revision resulting in RGS being classified as belonging to the genus *Urocitellus* (Helgen et al. 2009). The range of RGS extends across the North American short- and mixed-grass prairies in southern Canada (Saskatchewan, Alberta, and Manitoba) and the northern United States (Montana, North and South Dakota, and Minnesota) (Yensen and Sherman 2003). Although the geographic species range is known, little is known about how RGS are distributed within their range.

RGS are semi-fossorial and live in subterranean burrow systems that they construct. These burrow systems are usually 1 - 2 m deep and have multiple chambers and entrances (Michener and Koeppl 1985; Michener 2002). Each RGS hibernates alone, on average 0.5 m below ground in a chamber designated for this purpose (Michener 1992). RGS are colonial, living in matriarchal kin groups; more closely related females maintain burrows in closer proximity to one another (Yeaton 1972; Armitage 1981; Michener and Koeppl 1985). RGS are diurnal and spend 9-15 hours a day aboveground depending on the time of year (Michener 2002; Jones et al. 2009). Most of the time out of the burrow is spent foraging

(Michener 1979a; Michener and Koeppl 1985). They are primarily herbivorous, foraging mainly on the leafy vegetation, shoots, and seeds, of grasses and forbs, although, they are known to consume insects and scavenge road-killed con-specifics opportunistically (Howell 1938; Hansen and Ueckert 1970; Michener and Koeppl 1985). However, information on the diet and burrowing behaviour of RGS is based on research conducted after the conversion of most of the native prairie for human uses (e.g., agriculture) and not on what would historically have been their natural environment.

Although RGS populations can be active for up to 9 months of the year (February to October), individual squirrels are active for much shorter periods of time. RGS are obligate hibernators and individuals spend up to 8 months hibernating (Michener and Michener 1977; Michener 1992). Including time below ground during the active season, RGS spend as little as 15% of their lives aboveground (Michener 2002). Male and female emergence from hibernation is synchronous within sexes but asynchronous between sexes (Yeaton 1972; Michener 1977b; Michener 1983; Davis and Murie 1985). Time of emergence can vary by weeks based on the weather and the region (Michener 1977a; Michener 1979b; Michener 1983); however, time intervals of biological events remain consistent between years (e.g., time of emergence until mating, parturition, and emergence of juveniles; Michener 1985). In general, adult males emerge from hibernation around mid-February, followed by adult females, in mid-March; immergence into hibernation follows this same pattern (Michener 1979b; Michener 1992). Mating occurs shortly after adult female emergence and altricial juveniles are born

underground after a 23-day gestation period (Yeaton 1972; Michener 1980; Michener 1983; Michener 1985; Michener and Koeppl 1985). At one month old, juvenile males and females emerge simultaneously from their natal burrows (Michener 1985) and are active until September (females) and October (males) (Michener 1992). Because mating occurs over a short period of time for all RGS, the emergence of juveniles creates a rapid increase in the number of RGS that can be seen aboveground. This increase in abundance leads to the perception that RGS numbers are high and is often the catalyst for management actions; however, this increase is only temporary. Research is needed to identify factors that affect the long-term abundances of RGS populations rather than focusing on temporary fluctuations.

Each adult squirrel occupies its own home range. Although home range size varies seasonally, in general, the core area of an adult squirrel's home range covers ~ 225 m^2 (Michener 1979a). Adult male and female home ranges overlap early in the spring during mating (Yeaton 1972; Michener 1979a; Davis and Murie 1985). Male and female RGS are sexually mature at one year of age and females are capable of reproducing only once per year (Sheppard 1972; Michener 1983; Michener 1985; Jones et al. 2009). Juveniles dispersing from their natal burrow tend to show fidelity to their natal area and rarely disperse more than 200 m (Michener and Michener 1977; Davis and Murie 1985). The sedentary nature of RGS makes them a great candidate for monitoring programs; however, no such programs existed until recently, and only cover a small portion of their range. Monitoring programs could further our current understanding of RGS ecology as

well as provide insight into a wide array of interactions between RGS and the environment; such as their relationship with Species at Risk (SAR), vegetative communities, soil processes, and biodiversity.

Although RGS have multiple offspring in a litter, they are a prey species, and the survival rate of juveniles is low (approximately 30%/year; Michener 1989; Michener and Michener 1977). The number of offspring in a litter is related to female body condition (Sheppard 1972; Armitage 1981; Risch et al. 2007; Ryan et al 2012). Litter sizes can vary from 1 to 14 young but the most common number is 6 or 7 (Armitage 1981; Sheppard 1972; Risch et al. 2007; Jones et al. 2009). Generally, the juvenile sex ratio is 1:1, independent of litter size (although recent evidence has indicated larger litters are female-biased; Ryan et al 2012), while the adult sex ratio is female-biased with at least 3 females for every male (Nellis 1969; Sheppard 1972; Michener and Michener 1977; Michener 1989). Male RGS have a lower survival rate and a shorter lifespan than females (Michener and Michener 1971; Michener and Michener 1977; Michener 1989). On average, only 12% of males survive 1 year, 3% to 2 years old, and less than 1% of males survive to 3 years old, with the latter being their maximum lifespan (Michener 1989). While for females, an average of 46% survive to 1 year old, 27% to 2 years, and 17% to 3 years old, with their maximum lifespan being 6 years old (Michener 1989). The most common causes of mortality have been proposed to be predation, and over-winter/early spring mortality (Clarke 1970; Luttich et al. 1970; Michener and Michener 1977; Michener 1977a; Schmutz and Hungle 1989; Michener 2004), although the fate of missing individuals from populations is largely unknown.

1.2 Ecosystem Importance

RGS can have a pronounced effect on ecosystem processes. Large grazers contribute to soil compaction through trampling, whereas small burrowing mammals, such as RGS, increase soil aeration (Laundre and Reynolds 1993). RGS burrows can also affect the hydrology of the system due to increased water infiltration via tunnels and reduced soil erosion (Laundre and Reynolds 1993). Because RGS are colonial, their burrowing and grazing occurs in concentrated areas. Increased concentrations of nutrients and easily metabolized carbons produced by activities such as foraging, caching, urination, and defecation, can stimulate microbial growth and increase soil nitrogen availability (Ayarbe and Kieft 2000, Green and Detling 2000, Bakker et al. 2004). RGS produce small amounts of concentrated urine and feces which is spread over a greater area than that of larger grazers making it more easily broken down, more finely distributed, and more readily available for uptake by other organisms (e.g., plants and microbes) (Bakker et al. 2004). The high levels of soil disturbance caused by producing and maintaining burrows can also lead to increased microbial activities as nutrients and energy become well mixed (Ayarbe and Kieft 2000). Although they have the potential to significantly impact abiotic processes, specific information on these interactions is largely unknown for RGS.

RGS have the potential to alter vegetative structure that can result in improved nutritional quality of vegetation (Weltzin et al. 1997; Fahnestock and Detling 2002; Newediuk 2011). Smaller herbivores (e.g., rodents) yield higher levels of soil nitrogen mineralization that are maintained longer during the season

when compared to larger herbivores (e.g., ungulates) (Holland and Detling 1990; Fahnestock and Detling 2002; Bakker et al. 2004). This higher net nitrogen mineralization is occurring to a large extent as nitrification and nitrate accumulation, which is readily taken up by plants (Le Roux et al. 2003; Bakker et al. 2004). Although aboveground plant biomass is not increased by grazing (Green and Detling 2000; Fahnestock and Detling 2002; Newediuk 2011), plant nitrogen concentrations are increased (Green and Detling 2000). Particularly, increases in nitrogen levels are more pronounced in plant leaves than in stems, which increases the availability of plant nitrogen to grazers (Green and Detling 2000). Continual grazing of plants and high nutrient availability can also cause higher plant allocation of carbon aboveground for growth rather than belowground to roots (Ayarbe and Kieft 2000). In addition, RGS abundance increases plant species diversity; particularly increasing the proportion of higher quality forage species (Newediuk 2011). Although RGS remove aboveground biomass and, therefore, are viewed as competing with livestock for forage, their relationship with other grazers is complex. They may be reducing vegetation quantity, but RGS may in fact be increasing nutritional quality of the vegetation for livestock. Information on how RGS affect nutrient stimulation and their impact on vegetative nutrient acquisition, would be beneficial to assessing the impacts of RGS on other grazers, particularly livestock.

RGS also have the potential to significantly impact populations of many sympatric wildlife species. They are key components in food webs, serving as prey for many grassland vertebrate predators (Lacey 2000). For example, RGS make up

60-90% of the diet of many avian predators, including Swainson's hawks (*Buteo Swainsoni*), red-tailed hawks (*Buteo jamaicensis*), prairie falcons (*Falco mexicanus*), and ferruginous hawks (*Buteo regalis*), during the chick rearing period (Luttich et al. 1970; Schmutz and Hungle 1989; Hunt 1993; Schmutz et al. 2001). For ferruginous hawks, a threatened species in Canada (COSEWIC 2008), reductions in local RGS populations have been associated with decreased reproductive success (Schmutz and Hungle 1989). Coyotes (*Canis latrans*), long-tailed weasels (*Mustela frenata*), and badgers (*Taxidea taxus*) are also significant predators of RGS (Michener 1977a; Michener 2004). Badgers, in particular, can account for up to 90% of the mortality in a RGS population (Michener 2004). Understanding factors that affect the abundance and distribution of ground squirrels is important for maintaining biodiversity on the prairies; however, ecological and environmental influences on ground squirrel populations are poorly understood.

RGS are also important in providing habitat to a wide range of prairie species. Their burrows are used as shelter or nest sites for many grassland species of arthropods, amphibians, reptiles, birds, and mammals. For example, invertebrates, such as spiders, beetles, and bumblebees, as well as vertebrates, such as salamanders, snakes, rabbits, and foxes, will all take advantage of, and in some cases rely on, RGS burrows for nesting or retreat sites. Of particular importance are burrowing owls (*Athene cunicularia*) (Coulombe 1971; Martin 1973; Wellicome 1997; Poulin et al. 2005), eastern yellow-bellied racers (*Coluber constrictor flaviventris*) (Martino et al. 2012), and swift foxes (*Vulpes velox*) (Pruss 1999), which are all SAR in Canada (COSEWIC 2004; 2006; 2009). Despite the important

ecological associations between RGS and SAR, data on habitat selection by RGS are essentially non-existent.

1.3 Agricultural Pests

Humans have extensively modified prairie habitats for the purpose of agricultural crop production, often creating pest species by enabling wildlife that consume crops to flourish. Pest populations respond numerically to increases in food availability, and the damage they cause is the functional response to this increase (Puan et al. 2011). Predators can also increase as a response to increased prey availability, and subsequently reduce the prey population size (Rosenzweig and MacArthur 1963). However, humans also have a history of trying to eradicate predators (Fritts et al. 1994; Collinge 2009; Lavers et al. 2010). In the absence of predators, agricultural pest populations are not kept in check (Enari and Suzuki 2010) and are able to increase to levels that are difficult to manage (Hone 2007). Vertebrate pests have often been neglected in management of crops in favour of focusing on insects or diseases, but in cases where management takes place, it is often implemented after outbreaks (Van Vuren and Smallwood 1996; Fagerstone 2002). Reactionary, rather than preventative control efforts are less likely to be successful because bait effectiveness is often time-dependant and pest populations can become too high to respond to control in the desired time frame (Hone 2007).

Agricultural pests can have devastating effects on food production and have caused significant economic losses (Basri and Halim 1985; Enari and Suzuki 2010;

Puan et al. 2011). Mammalian pests, alone, can cause significant losses in agriculture (Saunders et al. 2010). Despite their important ecological value, RGS are regarded as pests in agricultural and urban communities due to their grazing and burrowing activities, and considerable efforts are expended to control or eradicate their populations (Fall and Jackson 1998; Bruggers et al. 2002; Government of Saskatchewan 2010). The economic costs of pests are not only through damage directly to crops, but also through competition for livestock forage, damage to property, and the costs associated with pest control (Saunders et al. 2010). For example, in 2008, the Saskatchewan Ministry of Agriculture paid $1.25 million in rebates to farmers for 50% of the cost of pest control products for RGS (Williamson 2009). Although they are considered agricultural pests, data on the economic costs associated with agricultural damage due to RGS do not exist.

Management of RGS as pests is viewed as a necessary process in agricultural production; however it can have negative consequences for native biodiversity and SAR. Extermination of entire RGS populations can have ecological impacts associated with loss of the squirrels. Destroying RGS populations is not only damaging to the squirrels themselves, but also removes them as a source of prey for native predators, particularly RGS specialist predators such as ferruginous hawks (Schmutz and Hungle 1989). Removal of RGS also eliminates the burrows they create, and thereby the species that rely on them, including SAR such as burrowing owls (Coulombe 1971; Martin 1973; Wellicome 1997; Poulin et al. 2005). In addition, pest control methods can amplify these negative effects on the environment (Berny 2007). There is a wide variety of

control methods used to minimize damage from mammalian pests. Careful selection of the intensity of control and appropriate control methods is important to minimizing the indirect negative effects that pest control can have on the ecosystem.

Poisoning is a common method used to control RGS but there are numerous negative effects associated with the use of poisons. Besides labour and economic costs involved with purchase and application, pesticide use poses health risks to humans and wildlife (Eason et al. 2010). The use of poisons can also cause economic losses through indirect damage to agricultural products. For example, an estimated loss of $30.8 million in livestock in the United States is caused by pesticide poisoning (Pimentel 2005). Chemicals used as rodenticides (e.g., strychnine) also cause mortality of non-target wildlife via unintentional or secondary poisoning (Berny et al. 1997; Knopper et al. 2006; Berny 2007; Proulx 2011). Many RGS predators, such as foxes and owls, are killed due to secondary poisonings (Shore et al. 1999). Removal of non-target species, which are often predators of the targeted species, results in less efficient pest management by indirectly reducing predation pressure on pests; therefore, precautions should be taken to reduce unintended mortality through the use of poisons.

Integrated pest management that combines traditional pest control practices with ecological-based methods, should be implemented in all pest management strategies. For example, methods of restoring natural predator populations, such as installing ferruginous hawk nest poles, could help control RGS numbers in areas where they are perceived to be causing damage (Schmutz and Hungle 1989;

Michener 2001). Cost-benefit analyses, comparing chemical versus ecological control methods and assessments of RGS damage, would provide insight into determining the most appropriate management actions, or if management is required at all, in different situations. Although control of RGS can have large impacts on the ecosystem, most studies focused on RGS have not been management-related, but rather are focused on behavioural ecology (Michener 1974; Michener 1979a; Davis 1982; Warkentin et al. 2001). There is a lack of research on the influence of environmental factors on RGS population biology. These data on essential habitats for RGS would help to reduce the negative impacts of pest control on other species through more efficient management practices, such as integrated pest management practices that would allow for a reduction in the use of rodenticides.

Both management and conservation of a species requires knowledge of its distribution, abundance, and life history traits. In particular, the habitat requirements of a species are important for management at the landscape-level (Clark et al. 1993; Gurnell et al. 2002; Gibson et al. 2004). Management strategies are often made based on post-hoc observations of pest densities as opposed to forecasts of potential problem areas (Hone 2007; Government of Saskatchewan 2008). Pest management that is applied only after there is a problem rather than pre-emptively has the potential to create a perpetually inefficient approach to managing RGS. Identification of habitat variables that affect RGS density can provide insight for control strategies and aid in focusing efforts on areas of highest concern. This would allow for preventative, rather than reactionary, management

actions proportional to their need, and the potential to mitigate the impacts on non-target species and the ecosystem.

1.4 Habitat Selection

Habitat selection by animals occurs when resources are used disproportionately to their availability (Manly et al. 2002). The distribution and abundance of a species can be used to infer habitat selection, based on the spatial distribution of the animals in relation to the spatial distribution of habitat variables (Osborne et al. 2001). A resource selection function (RSF) model can be used to determine the probability of habitat use by a species (Boyce et al. 2002; Manly et al. 2002). Comparing locations used by animals with unused locations is a common method to infer habitat selection using RSF models (Manly et al. 2002). Using the resource dependence of a species based on habitat selection, RSF models can also be used to predict and map the distribution and abundance of a species in future years, or across areas where their presence and density is unknown (Boyce and McDonald 1999; Meyer and Thuiller 2006). The accuracy of these models is dependent upon the number and spatial arrangement of locations sampled (Meyer and Thuiller 2006; Heywood et al. 2011). Despite the utility of RSFs to conserve and manage wildlife through predictive models, they have not been constructed for many species.

Research on habitat selection would be beneficial to management and conservation of RGS as a species. Identification of habitat features (and their

interactions) that support high densities of RGS could result in the ability to use general habitat modification as a pest management technique. This may reduce the necessity to poison or exterminate RGS populations, and therefore, reduce the associated negative effects on SAR and other wildlife. Research is needed to determine factors that affect RGS densities to aid in developing management strategies based on habitat modification. Although predictive habitat selection models would be useful for the development of management and conservation strategies for RGS in particular, this technique has not been implemented for this species.

Information on RGS habitat associations is lacking; however, there are several major factors that likely contribute to their abundance and distribution. Spatial variation in environmental variables such as soil composition, and differences in land use practices, land cover, and vegetation structure, all likely influence distribution and abundance. These variables have been shown to affect populations of other species similar to RGS in physiology, life history, and/or placement on the landscape (Feldhamer 1979; Geier and Best 1980; Rosenstock 1996; Ball et al. 2005). For example, vegetation and substrate type were the primary factors affecting the occupancy of Palm Springs ground squirrels (*Xerospermophilus tereticaudus chlorus*) in California (Ball et al. 2005). Arctic ground squirrels (*Urocitellus parryii*) were found to be associated with well drained substrates and avoided forested areas (Barker and Derocher 2010). RGS occur across a vast and diverse area of the northern Great Plains that includes several ecoregions with differences in climate and geology. Their range includes multiple

land use types, native grass, tame grass, cereal crops, hay fields, and urban environments. However, there is no record of how they are distributed within their range and what factors affect their abundance.

1.5 Survey Methods

The four most common methods to survey for ground squirrels are: 1) burrow counts; 2) mark-recapture; 3) point counts; and 4) alarm call-playbacks, where point counts are conducted with the aid of a RGS alarm call. Burrow counts are the least expensive method, but they are not reliable predictors of RGS densities (Van Horne et al. 1997). Mark-recapture is the most accurate method, but it has the highest costs in terms of labour and equipment, and data can only be collected for relatively small areas (Van Horne et al. 1997). Visual counts of RGS recorded from repeated point counts in an area are correlated with RGS population densities estimated using mark-recapture methods (Fagerstone 1983). However, alarm call-playbacks result in higher detection of RGS and increased estimates of abundance (Downey et al. 2006). Upon detection of a terrestrial predator, RGS typically respond with a vigilant posture (standing erect) and emitting a repeated whistle alarm call (Davis 1984). Therefore, using terrestrial predator alarm call-playbacks enhances the ability to visually detect RGS during point counts, and should be considered the preferred method for conducting RGS surveys (Downey et al. 2006).

1.6 Study Objectives

The overall purpose of my research was to identify factors that influence the distribution and abundance of RGS across a prairie landscape used in multiple ways (e.g., crop production, pasture etc.). I hypothesized that RGS abundance and distribution would be variable across the landscape and influenced by extrinsic factors. I predicted that habitat features such as local land use, land cover, soil texture, and vegetation height would influence RGS presence and density. My data are intended to provide information to aid in both conservation of the prairie ecosystem, as well as development of effective, long-term, management practices for RGS.

The specific objectives of my research were to:

1) Determine how RGS are distributed, in terms of presence and abundance, across a broad scale in the core of their range.

2) Determine if habitat selection by RGS is occurring and, if so, which predictors best differentiate used and unused locations (presence / absence).

3) Determine if there is a relationship between environmental variables and RGS abundance, and which variables have the strongest influence on RGS abundance.

2. METHODS

2.1 Study Design

I performed broad-scale surveys in 2011 and 2012 to collect presence and abundance data for RGS and associated habitat measurements. I employed a used versus unused design to determine whether or not there was a difference in habitat characteristics at sites with RGS present versus unused sites (Boyce et al. 2002; Manly et al. 2002). Locations where RGS were detected were designated as used sites and locations where RGS were not detected were designated as unused sites. Habitat variables were also analyzed to determine whether or not they influence the abundance (as opposed to presence / absence) of RGS. Thus, habitat variables were compared to abundance data using only locations where RGS were detected. In 2012, additional searches to locate larger colonies were conducted. These colony searches were performed to allow me to determine habitat selection at locations with higher RGS abundances. A used versus unused design was also used for the colony surveys. Used and unused locations were paired, as sites where RGS were detected and sites with no detections (*see Colony Survey Site Selection*).

2.2 Surveys

2.2.1 Broad-scale Survey Site Selection

I undertook surveys in an area covering 130,000 km^2 at the core of the Richardson's ground squirrel species range (Figure 1). I divided the area into 25 x 25-km quadrats and placed a 16-km transect along a road near the centre of every second quadrat. Transect orientation alternated between running north-south and east-west among the grid rows. Survey plots were placed at 1.6 km intervals (=10 points) along transects. This scale was selected to match the legal land division system such that counts took place in the middle of every second quarter section along the transect. RGS counts and habitat measurements were conducted in a 200 x 200-m plot directly adjacent to the road with the observer in the middle of the outside edge.

In 2011, 49 transects were surveyed in the eastern half of the study area between 4 June - 20 June, and 45 transects were surveyed in the western half of the study area between 26 July - 10 August. In 2012, all north-south running transects from the 2011 sites (n=48) were re-surveyed twice: once between 3 - 29 June, and again between 7 - 24 August. Dates were chosen to avoid periods of population fluctuation such as emergence of juveniles (Michener 1992). We did not re-survey east-west running transects in 2012. In total, 1900 broad-scale survey plots were completed, distributed approximately equally between 2011 and 2012 (Table 1).

Table 1. Summary of Richardson's ground squirrel (RGS) broad-scale surveys conducted during 2011-2012. Surveys were undertaken in 4 ha plots. Used sites are locations where RGS were detected; density was determined using data from used sites only.

	Survey Plots	**Used Sites**	**Total RGS**	**RGS/ha**
2011	940 (49%)	94 (60%)	326 (62%)	0.87
2012	960 (51%)	63 (40%)	197 (38%)	0.78
TOTAL	**1900**	**157**	**523**	**0.83**

2.2.2 Colony Survey Site Selection

Colonies were identified opportunistically via observations from roads and through landowner communications. I considered a site a colony if ≥ 5 RGS were detected within a 200 x 200-m area. For each colony site, an adjacent site with no RGS detected, either in the field directly across the road (most cases) or north of the used site (if RGS were detected in the field across the road) was paired for comparison with the used site. Surveys for both the used and unused locations were conducted in 200 x 200-m plots adjacent to the road, except for a few cases where the colony was found > 200 m from the road. In such cases the 200 x 200-m plot was centred around the approximate centre of the colony, based on burrow placement and above ground RGS activity.

2.2.3 RGS Surveys

The number of RGS was determined at each survey plot using a call-playback method (Downey et al. 2006). The area was scanned with binoculars for a minimum of 30 seconds and continued until all visible RGS were counted or a full scan of the area was complete (Fagerstone 1983). A wildlife caller (FoxPro Spitfire, sound pressure level 102-106 dB) programmed with a RGS alarm call (repeated whistles; provided by Dr. James Hare, Biology Department, University of Manitoba) was played for the duration of the count, causing squirrels to stand up/call back (Davis 1984; Hare and Atkins 2001; Warkentin et al. 2001). Surveys were performed in good weather conditions (e.g., no precipitation, wind < 40 km/h,

temperature < 30°C; Michener 1968; Michener and Koeppl 1985; Michener 2002; Downey 2003). In addition, all surveys were conducted at least 75 minutes after sunrise/before sunset and the majority of surveys (84%) did not occur between noon and four, to coincide with peak periods of RGS activity (Michener 2002).

2.3 Habitat Measurements

For each 200 x 200-m survey plot in both broad-scale and colony surveys, I recorded vegetation height, land cover, land use, and distances to water, shrubs, trees, and buildings/structures. Vegetation height was recorded as the average of four measurements of vegetation types that best represented the proportions of land cover types present within the plot. Percent of each land cover type was estimated visually for each plot at 5% increments; this included water, shrubs, trees, grass, bare ground, or crop and the number of different cover types present was recorded as the cover diversity for that plot. Land use was recorded as one of seven categories: 1) native grass; 2) tame grass; 3) stubble crop; 4) hay crop; 5) tilled crop (a fallow field); 6) annual crop (e.g., wheat, barley, canola, mustard, flax, peas, etc.); or 7) other. The distance to the nearest water, shrubs, trees, and buildings/structures was recorded using a rangefinder (Bushnell Scout 1000) (as one of three categories: 1) within the survey plot; 2) not within the plot but present within 200 m from the plot boundary; or 3) greater than 200 m from the plot boundary. Soil texture was also incorporated into the dataset using a geographical information system (GIS) layer from Soil Landscapes of Canada (SLC 2010) which

classified soils into 5 categories: 1) moderately coarse; 2) medium; 3) moderately fine; 4) fine; and 5) very fine.

2.4 Statistical Analysis

Broad-scale presence and abundance data were analyzed using generalized linear mixed models (GLMMs), which included random effects that allowed me to control for repeated transects, surveys performed at different times throughout the summer and across years, as well as multiple observers (Bolker et al. 2009). Because surveys resulted in an unequal number of used to unused locations, a separate analysis was conducted by randomly selecting an equal number of unused locations. The results obtained did not differ (data not shown), so I report results from my analysis of the complete original dataset. Colony used-unused data were also analyzed using GLMMs to account for the pairing of used and unused sites. The paired sites were each given a matching Pair ID, which was used as a random effect. Abundance data from the colony surveys were analyzed using generalized linear models (Guisan et al. 2002). For both broad-scale and colony datasets, used-unused data were analyzed using a binomial distribution, whereas abundance data were analyzed using a Poisson distribution.

Model selection was performed using Akaike's Information Criterion (AIC) with correction for small samples where applicable (AICc; Akaike 1973; Hurvich and Tsai 1989; Burnham and Anderson 2002). All variables were tested

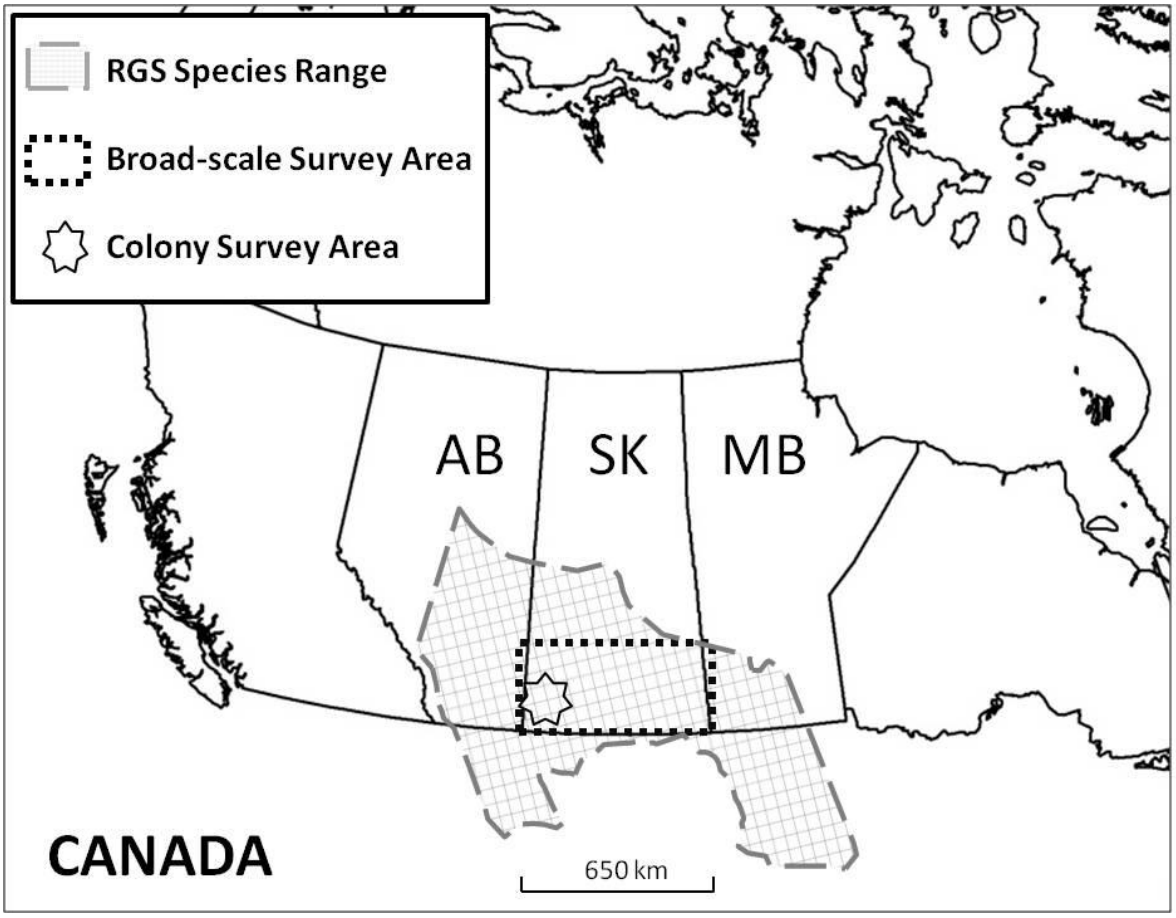


Figure 1. Richardson's ground squirrel (RGS) species range. Study areas selected for broad-scale surveys conducted in 2011 and 2012 and colony surveys conducted in 2012 are indicated.

univariately and those that did not perform better than the null model were removed (Arnold 2010). As well, when any two variables were highly correlated ($r > 0.7$), the variable with the lower delta AIC in a univariate model was removed. The remaining variables were evaluated in all possible combinations to determine the best explanatory model. In the case where multiple models competed for the top position (delta AIC ≤ 2), model averaging was used to determine which variables had the greatest influence among the models (Burnham and Anderson 2002; Grueber et al. 2011). All data were analyzed using the statistical program R version 2.15.2 (R Core Team 2012), with lme4, arm, and MuMIn packages (Bates et al. 2012; Gelman and Su 2013; Barton 2013). Means are presented ± 1 standard error.

3. RESULTS

3.1 Surveys

3.1.1 Broad-scale surveys

RGS were not distributed evenly across the landscape in either presence or abundance. There were large tracts of land in which RGS were not detected at all (Figure 2). RGS presence was much lower than expected across the province with only 8 percent of the survey plots having RGS (Table 1). Both RGS presence and abundance were highest in the Mixed Grassland ecoregion (70% and 78% respectively), particularly along the transition zone from the Mixed to the Moist Mixed Grassland ecoregion (Figure 2). RGS presence and abundance also decreased from 2011 to 2012, by 33% and 40%, respectively. Overall, abundance at used sites ranged from 1 (0.25/ha) to 35 (8.75/ha) with an average of 3.3 ± 0.4 RGS (0.83 ± 0.1/ha), while the total abundance, including unused sites, was 0.3 ± 0.0 RGS (0.07 ± 0.0/ha).

3.1.2 Colony surveys

In 2012, 31 colony sites were located and paired with adjacent unused sites. Overall, 314 RGS were counted at colony locations with an average of 10.1 ± 1.0 RGS per used site (2.5 ± 0.2/ha) (Figure 3). The maximum number of RGS counted at a used colony location was 47 (11.75/ha).

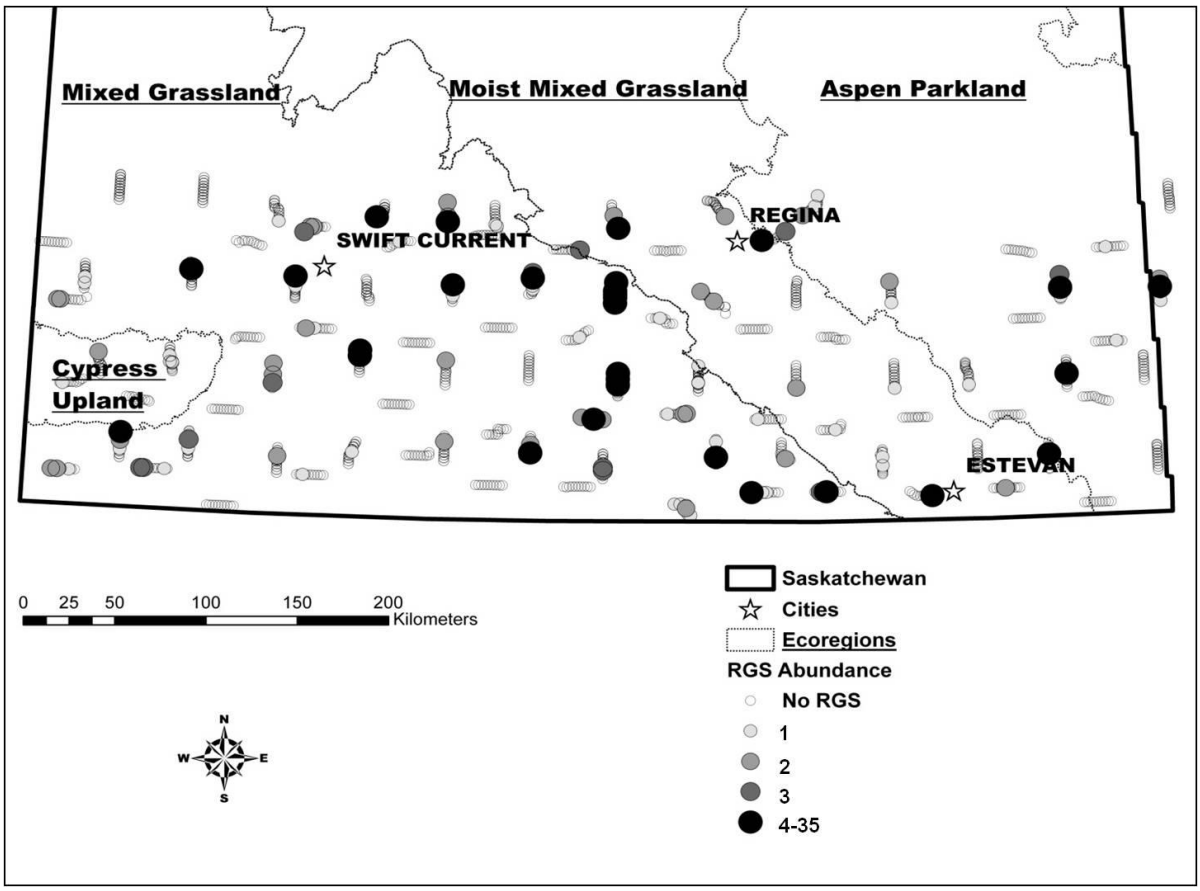


Figure 2. Richardson's ground squirrel (RGS) presence and abundance in different prairie ecoregions based on broad-scale surveys conducted in 2011 and 2012. Surveys were undertaken in 4 ha plots. Cut off values for abundances correspond with percentiles and critical values in the data: the minimum number of RGS and the 25th percentile of the abundance data = 1; 50th percentile = 2; 75th percentile and the mean = 3; and the maximum number of RGS = 35.

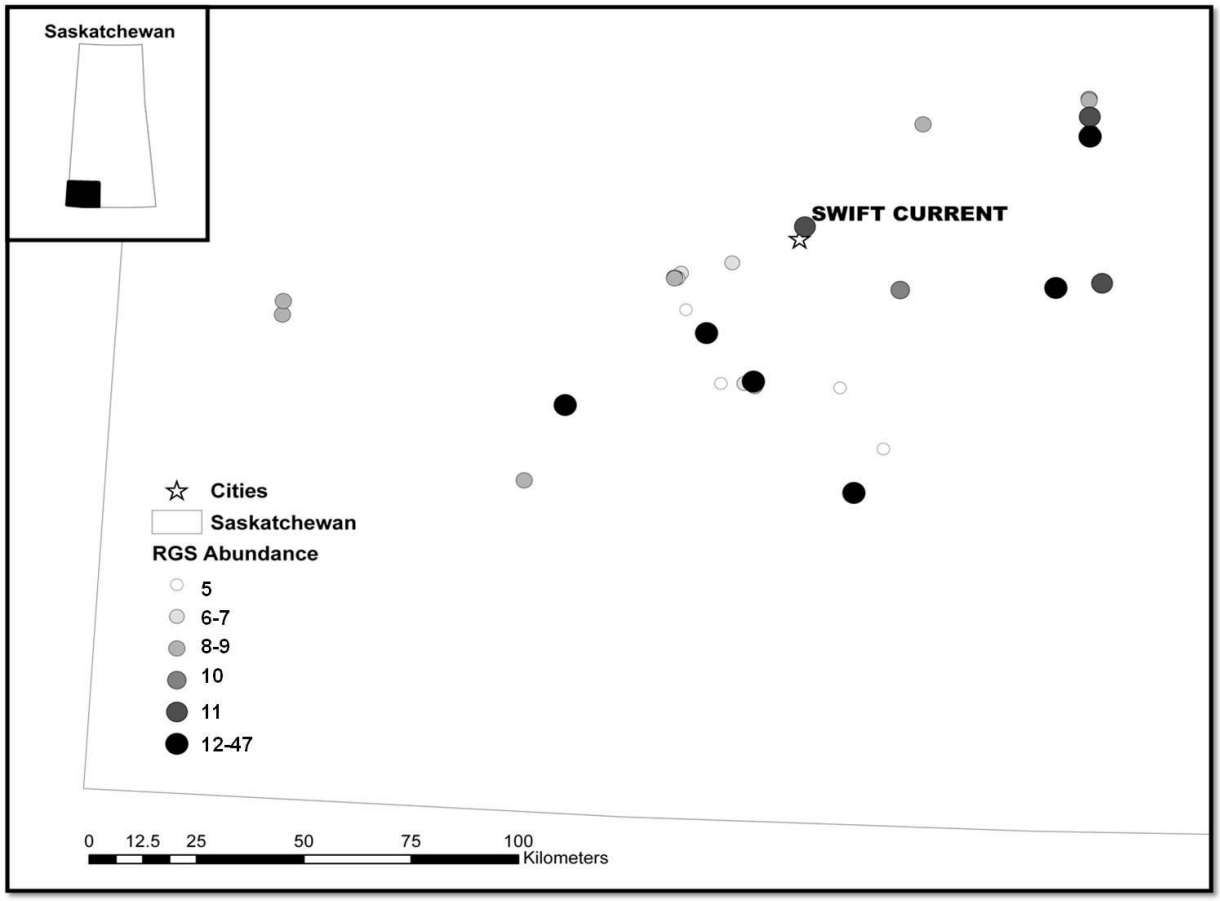


Figure 3. Richardson's ground squirrel (RGS) 2012 colony locations and abundances in southwestern Saskatchewan. Colony locations resulted from searches for sites with ≥ 5 RGS. Surveys were undertaken in 4 ha plots. Cut off values for abundances correspond with percentiles and critical values in the data: the minimum number of RGS = 5; 25th percentile of the abundance data = 7; 50th percentile = 9; the mean = 10; 75th percentile = 11; and the maximum number of RGS = 47.

3.2 Habitat Measurements

3.2.1 Broad-scale surveys: Presence

The top model that best explained RGS presence included percent cover of grass and the distance to trees (Table 2). RGS presence was positively affected by the percentage of grass cover and negatively affected by close proximity to trees. The mean percent cover of grass at used locations (46% ± 3.0) was more than 1.5 times that of unused locations (30% ± 0.8). The probability of RGS presence increased as percent grass cover increased regardless of the proximity of trees (Figure 4). RGS were found least frequently (22%) when trees were within the survey plot and more frequently (31%) when trees were not within the plot but within 200 m of the plot boundary. Unused locations showed the opposite trend. The frequency of unused locations where trees were within the plot was higher (27%) than when trees were within 200 m of the plot boundary (23%). Correspondingly, the model-predicted probability of habitat use by RGS was lowest when trees were present within the survey plot and highest when trees were absent from the plot but within 200 m of the plot boundary (Figure 5). Trees absent or at least 200 m from the plot boundary was the most frequent category for both used and unused sites (47% and 50%, respectively); thus, the predicted probability of RGS presence was intermediate for this category.

Table 2. Summary of top models for Richardson`s ground squirrel presence and abundance, at two different scales. Broad-scale surveys were performed in 2011 and 2012, and colony surveys were performed in 2012. All models performed better than the null (intercept-only) model.

Response	Model	K*	ΔAICc	Weight
Broad-scale				
Presence	Percent Grass + Distance To Trees	7	0	0.87
	Null	4	31.7	0
Abundance	Distance To Shrubs + Distance To Water + Land Use + Soil Texture + Vegetation Height + Percent Shrubs + Cover Diversity	20	0	0.32
	Distance To Shrubs + Distance To Water + Land Use + Soil Texture + Vegetation Height + Percent Shrubs + Percent Bare	20	0.2	0.30
	Distance To Shrubs + Distance To Water + Land Use + Soil Texture + Vegetation Height + Percent Shrubs	19	0.95	0.20
	Distance To Shrubs + Distance To Water + Land Use + Soil Texture + Vegetation Height + Percent Shrubs + Cover Diversity + Percent Bare	21	1.01	0.19
	Null	4	136.41	0.00
Colony				
Presence	Vegetation Height + Percent Bare Ground	4	0	0.67
	Null	2	44.2	0.00
Abundance	Vegetation Height	2	0	0.61
	Null	1	5.2	0.05

*Number of parameters

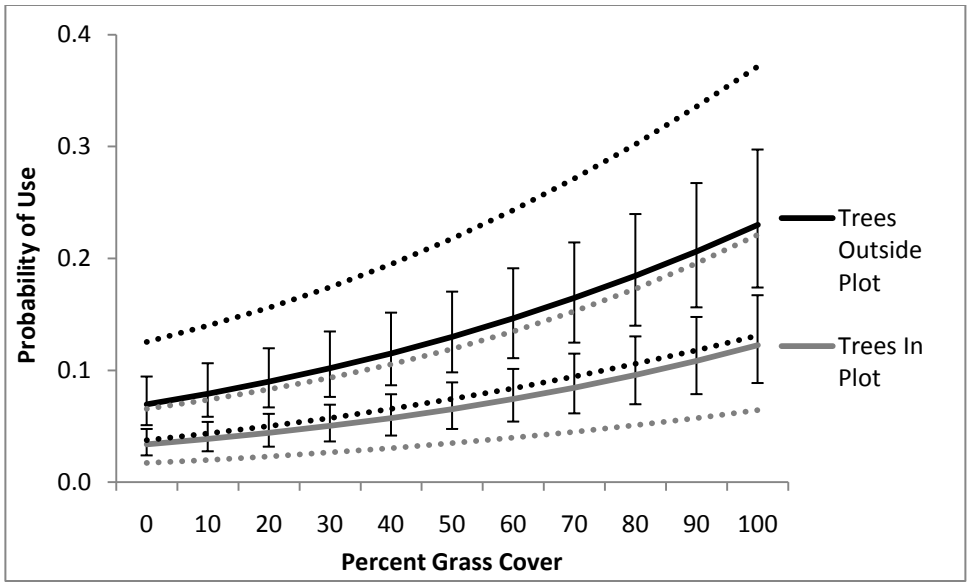


Figure 4. Predicted probability (±SE) (solid line), with 95% confidence intervals (dashed lines), of habitat use by RGS with varying amounts of grass cover. Model predictions are presented with trees present in the survey plot, and trees absent from the plot but present within 200 m. Data for the models are from 2011 and 2012 broad-scale surveys.

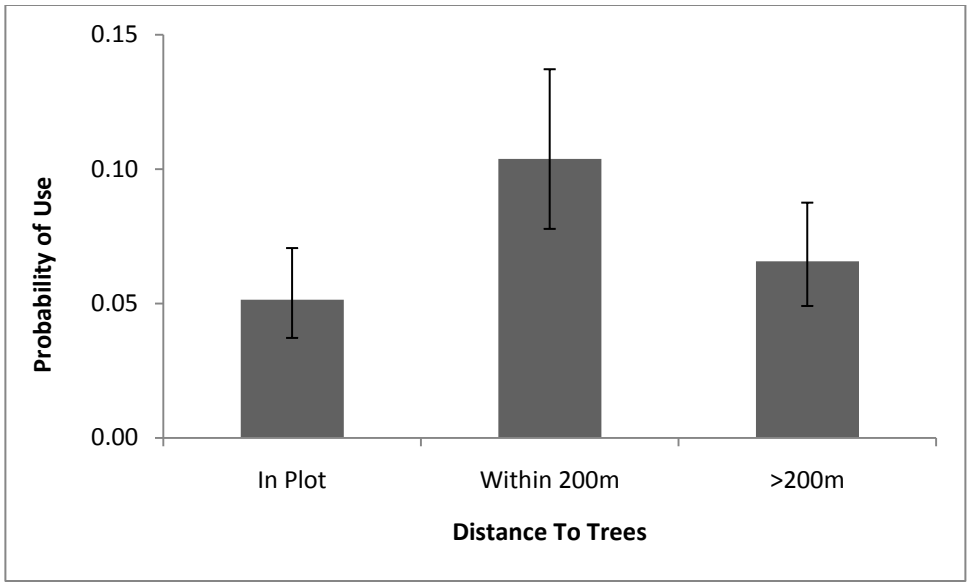


Figure 5. Probability (±SE) of habitat use by Richardson's ground squirrels for each category for distance to trees from 2011 and 2012 broad-scale survey data.

3.2.2 Broad-scale surveys: Abundance

RGS abundance was influenced by many habitat variables (Table 2). Four candidate models including 8 habitat variables competed as the top model. Model averaging determined that 6 of the 8 variables had equally high importance among the competing models (Table 3). The 6 variables that best explained RGS abundance at a broad scale were distance to shrubs, distance to water, land use, soil texture, vegetation height, and percentage cover of shrubs. The two variables that had the least influence were cover diversity and the percentage of bare ground. Mean and predicted RGS abundance was negatively affected by close proximity to shrubs and water. When shrubs were absent from the plot but within 200 m, the predicted number of RGS was more than double than that predicted when shrubs were in the survey plot (Figure 6). The predicted number of RGS when water was absent from the plot but within 200 m was also higher (almost double) than the number of RGS predicted when water was present in the survey plot (Figure 7).

Considering only used sites, the mean number of RGS per land use type from highest to lowest abundance was: tilled crop; tame grass; stubble crop; hay; annual crop; and native grass (Figure 8a). Predicted RGS abundance was highest in tilled crops, followed by tame grass, hay, and stubble crops. The lowest abundance predicted was for annual crops; abundance in native grass was not predicted as this category was the reference value for predictions of the other land use types (Figure 8b). Mean and predicted number of RGS was highest in very fine soils and decreased as soil texture became coarser. There was more than a 10-fold difference

between the highest and lowest predicted number of RGS based on soil type (Figure 9).

Vegetation height negatively affected RGS abundance. Both the number of RGS counted during surveys and the model predicted number of RGS decreased with increased vegetation height (Figure 10). The average vegetation height was 20.9 ± 2.1 cm for all sites with above average RGS abundance while locations with lower abundances had an average height that was nearly double (37.7 ± 3.4 cm). In addition, there was a larger decrease in the model predicted abundance for vegetation heights between 0 and 30 cm than for higher intervals. The highest predicted RGS abundance occurred when vegetation height was 0 cm and decreased by 25% at a height of 15 cm. At 30 cm the maximum model predicted abundance was only half (44% decrease in the predicted number of RGS). Higher vegetation heights continued to reduce the predicted number of RGS but to a lesser extent (an additional 0-15% decrease per 15 cm increase in vegetation height). RGS abundance was also negatively affected by percentage cover of shrubs. The number of RGS counted during surveys as well as the predicted RGS abundance decreased with an increase in percent shrub cover (Figure 11). Percent cover of shrubs was ≤ 10% for all sites with above average RGS counts, while shrub cover reached 30% for used sites with less than average numbers of RGS. Predicted RGS abundance showed a larger decrease (47%) for shrub cover between 0 and 10% than for higher intervals (< 15%), and levelled off at 0 RGS predicted after approximately 30% shrub cover.

Table 3. Model averaging results for Richardson's ground squirrel abundance from broad-scale surveys. Effect sizes have been standardized for direct comparison. Confidence intervals are at the 95% level.

Relative Importance	Parameter	Category	Estimate	SE	Lower CI	Upper CI
	(Intercept)		0.64	0.48	-0.30	1.57
1.00	Distance To Shrubs	In Plot	0.40	0.22	-0.03	0.82
		Within 200 m	-0.47	0.17	-0.81	-0.14
		> 200 m			*reference category*	
1.00	Distance To Water	In Plot	0.11	0.23	-0.33	0.55
		Within 200 m	-0.55	0.24	-1.01	-0.09
		> 200 m			*reference category*	
1.00	Land Use	Tame	-0.04	0.20	-0.43	0.34
		Stubble Crop	-0.39	0.25	-0.89	0.10
		Hay	-0.66	0.23	-1.11	-0.21
		Tilled Crop	0.43	0.31	-0.18	1.04
		Annual Crop	0.01	0.28	-0.54	0.56
		Native			*reference category*	
1.00	Soil Texture	Medium	-0.17	0.44	-1.03	0.68
		M Fine	0.13	0.43	-0.71	0.97
		Fine	0.81	0.50	-0.17	1.80
		V Fine	2.14	0.50	1.16	3.13
		M Coarse			*reference category*	
1.00	Vegetation Height		-0.91	0.19	-1.28	-0.54
1.00	Percent Shrubs		-0.59	0.19	-0.95	-0.22
0.51	Cover Diversity		-0.43	0.27	-0.96	0.09
0.49	Percent Bare		-0.25	0.17	-0.59	0.08

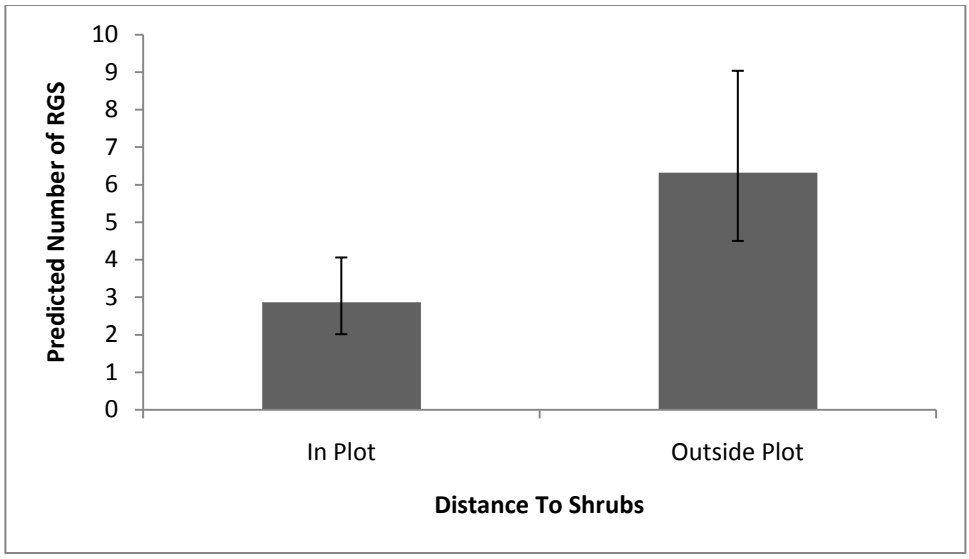


Figure 6. Predicted (±SE) number of Richardson's ground squirrels (RGS) at used sites for different categories of distance to shrubs. Data are from 2011 and 2012 broad-scale surveys. A third category for shrubs absent (> 200 m from the plot boundary) was a reference value for calculating the fixed effects for the other categories and therefore does not have a predicted value.

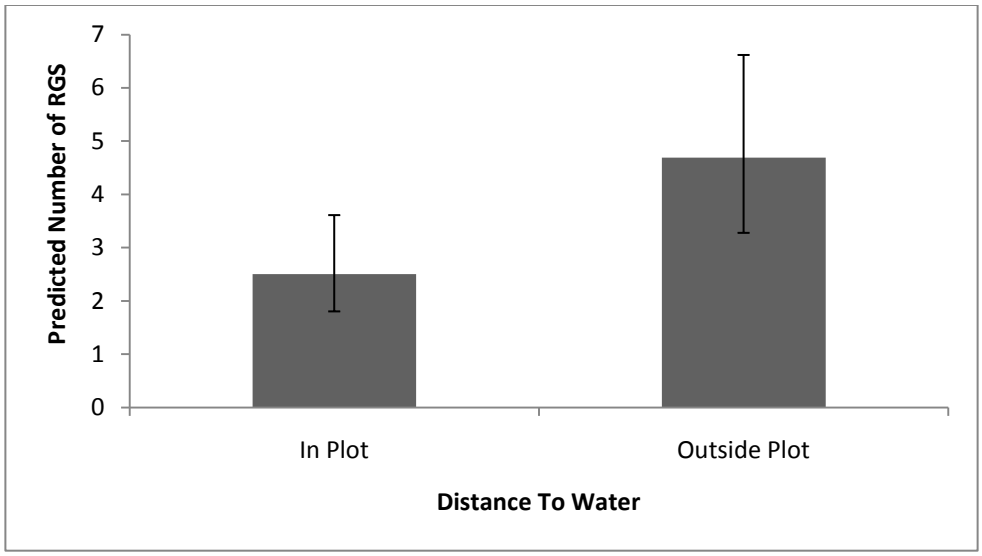
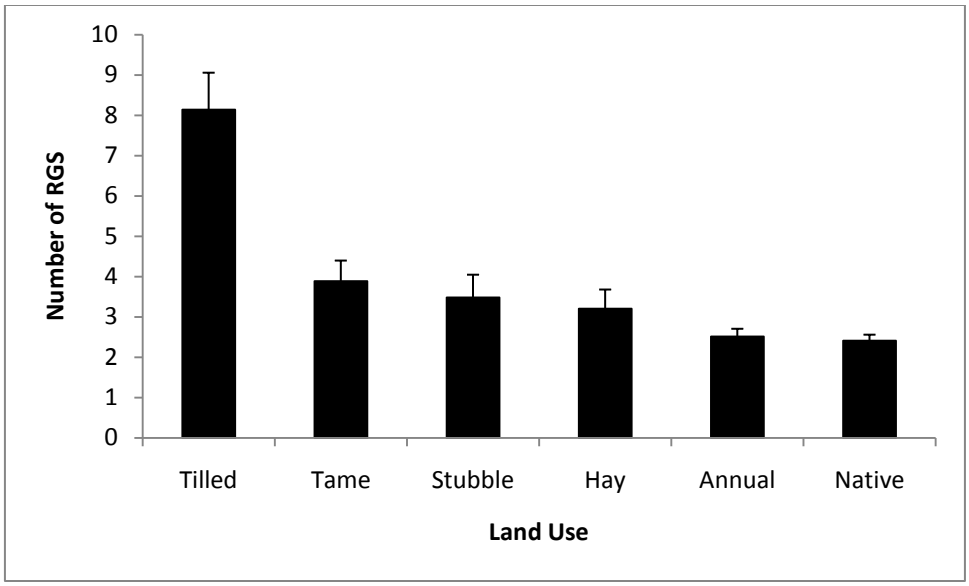
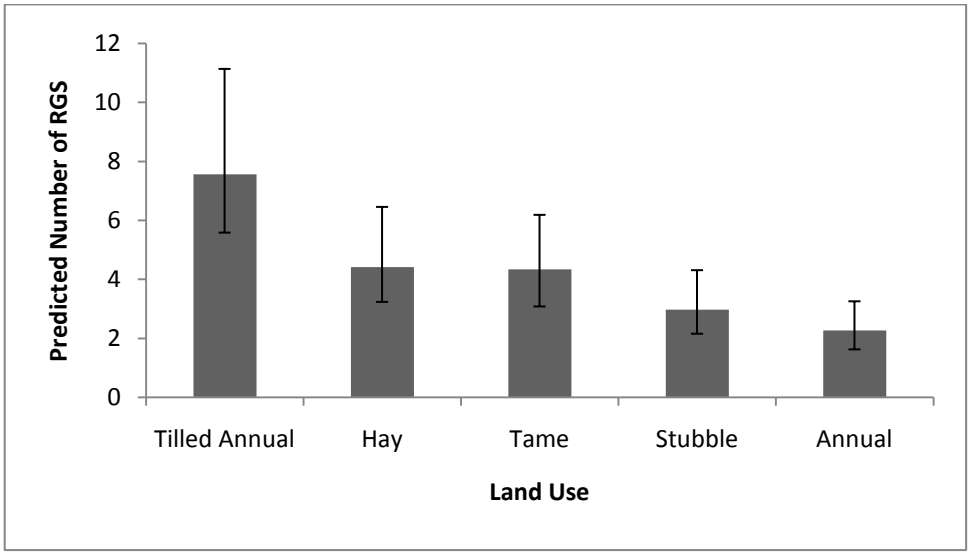


Figure 7. Predicted (±SE) number of Richardson's ground squirrels (RGS) at used sites for different categories of distance to water from 2011 and 2012 broad-scale surveys. A third category for water absent (> 200 m from the plot boundary) was a reference value for calculating the fixed effects for the other categories and therefore does not have a predicted value.



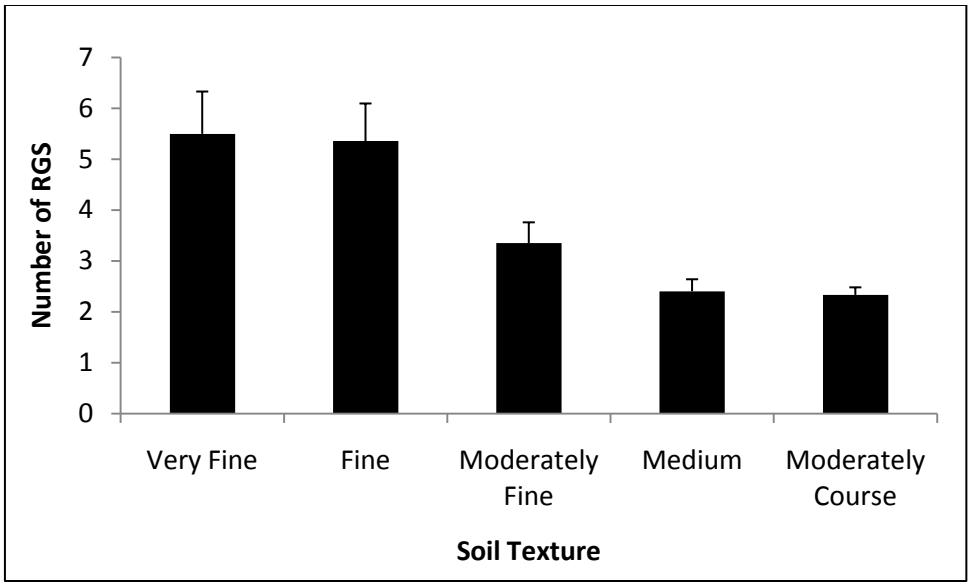
(a)



(b)

Figure 8. Mean (SE) (a) and predicted (±SE) (b) number of Richardson's ground squirrels at used sites for each land use category from 2011 and 2012 broad-scale surveys. A sixth category for native grass was a reference value for calculating the fixed effects for the other categories and therefore does not have a predicted value.

(a)



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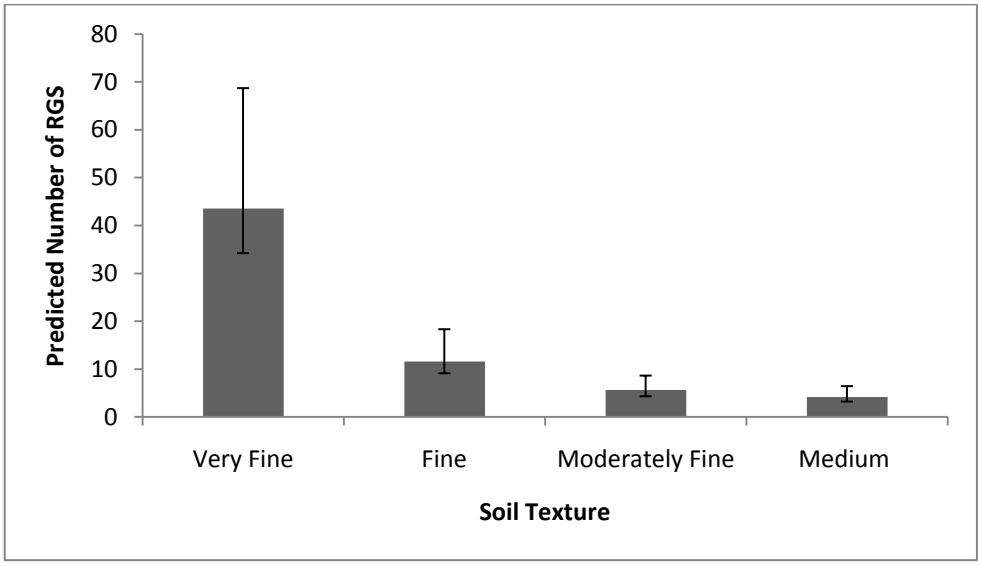
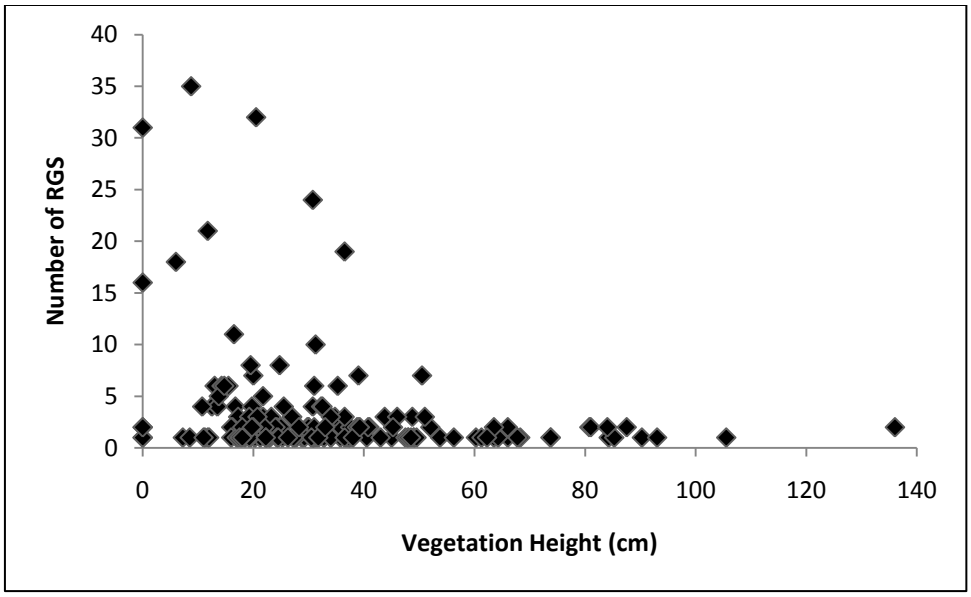
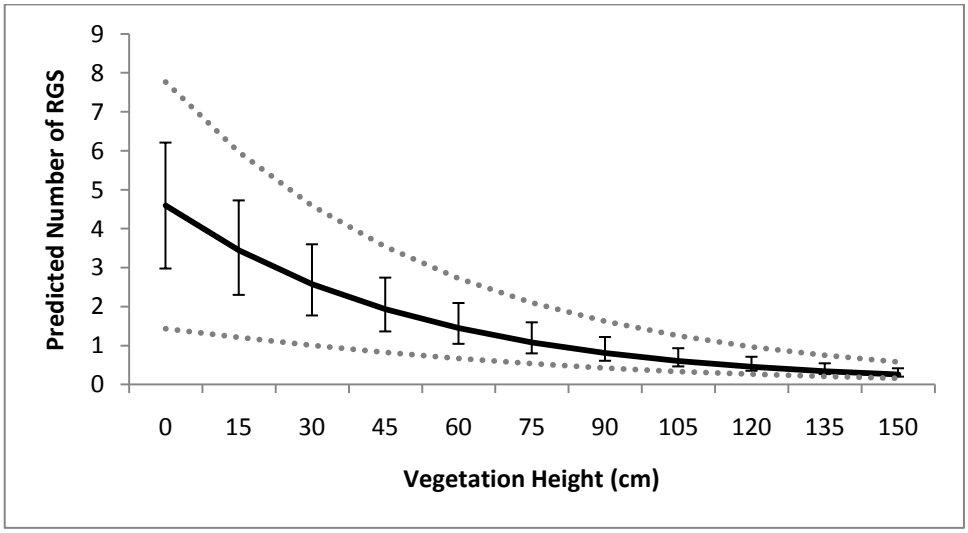


Figure 9. Mean (SE) (a) and predicted (±SE) (b) number of Richardson's ground squirrels at used sites for each soil texture category from 2011 and 2012 broad-scale surveys. A fifth category for moderately coarse soil texture was a reference value for calculating the fixed effects for the other categories and therefore does not have a predicted value.

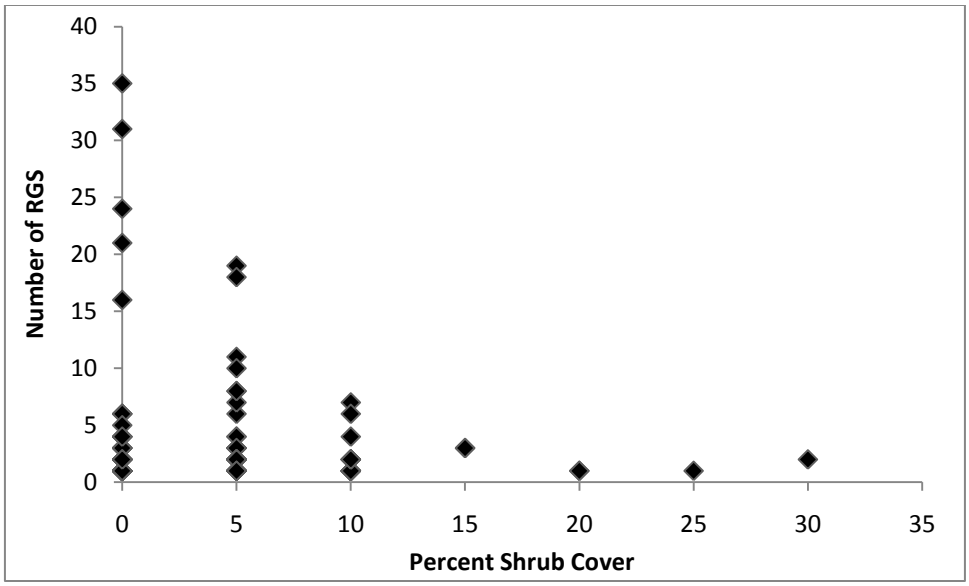


(a)

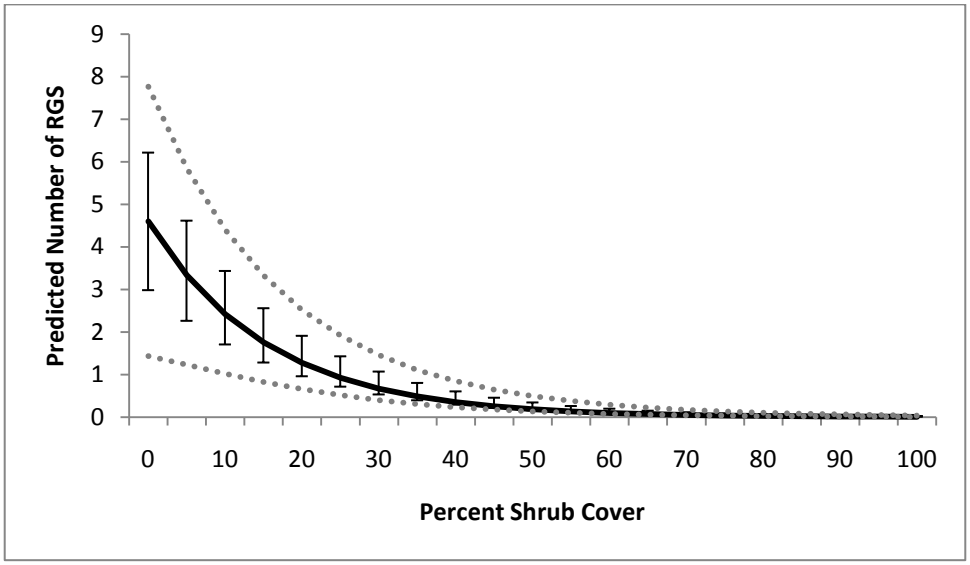


(b)

Figure 10. Richardson's ground squirrel (RGS) abundance (±SE) at varying vegetation heights: (a) observed at used sites and (b) model predicted (solid line) with 95% confidence intervals (dashed lines). Data are from broad-scale surveys in 2011 and 2012.



(a)



(b)

Figure 11. Richardson's ground squirrel (RGS) abundance (±SE) at varying amounts of shrub cover: (a) observed at used sites and (b) model predicted (solid line) with 95% confidence intervals (dashed lines). Data are from broad-scale surveys in 2011 and 2012.

3.2.3 Colony surveys: Presence

The variables that best explained the difference between used and unused locations were vegetation height and percentage of bare ground (Table 2). Vegetation height negatively affected RGS presence while percent bare ground had a positive influence. The mean vegetation height at sites used by RGS (24 cm ± 1.8) was 2.5 times lower than that of unused locations (60 cm ± 4.6). The probability of use by RGS decreased with increasing vegetation height; only a 4% decrease occurred as vegetation increased from 0 cm to 15 cm, while the largest decrease (44%) occurred between 30 and 45 cm (Figure 12). The predicted probability of use by RGS reached zero at a vegetation height of 60 cm. Although the percentage of bare ground was low at both used and unused locations, on average percent bare ground was higher at used sites (5% ± 1.7) than unused locations (1% ± 0.4). As well, the percent bare ground had a larger range among used sites (0 - 50%) than among unused locations (0 - 5%). The predicted probability of habitat use by RGS increased with percent bare ground steeply from 0 to about 10% bare, and levelled off at the maximum possible probability of 1.0 when percent bare ground reached 25% (Figure 13).

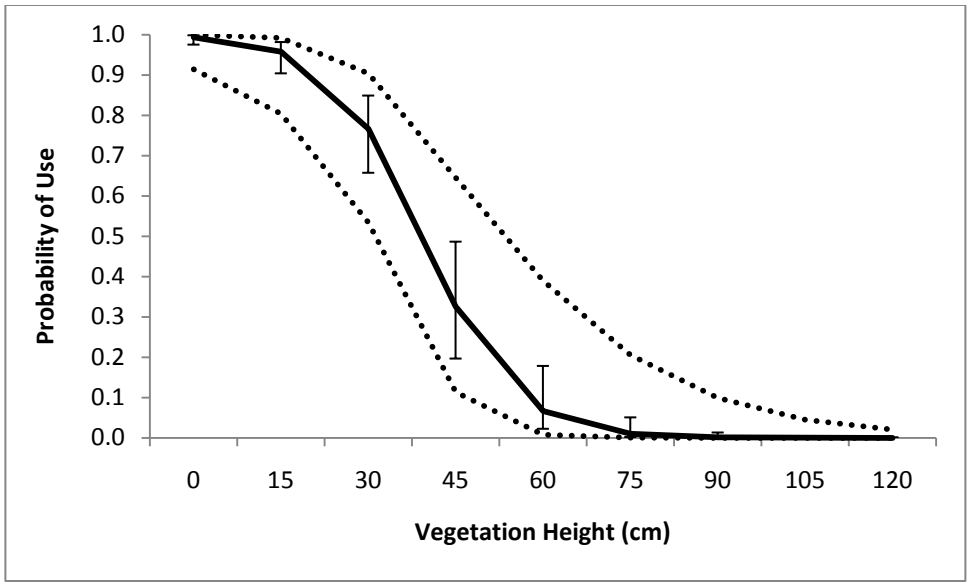


Figure 12. Predicted probability (±SE) (solid line), with 95% confidence intervals (dashed lines), of habitat use by Richardson's ground squirrels with varying vegetation height, based on data from 2012 colony surveys.

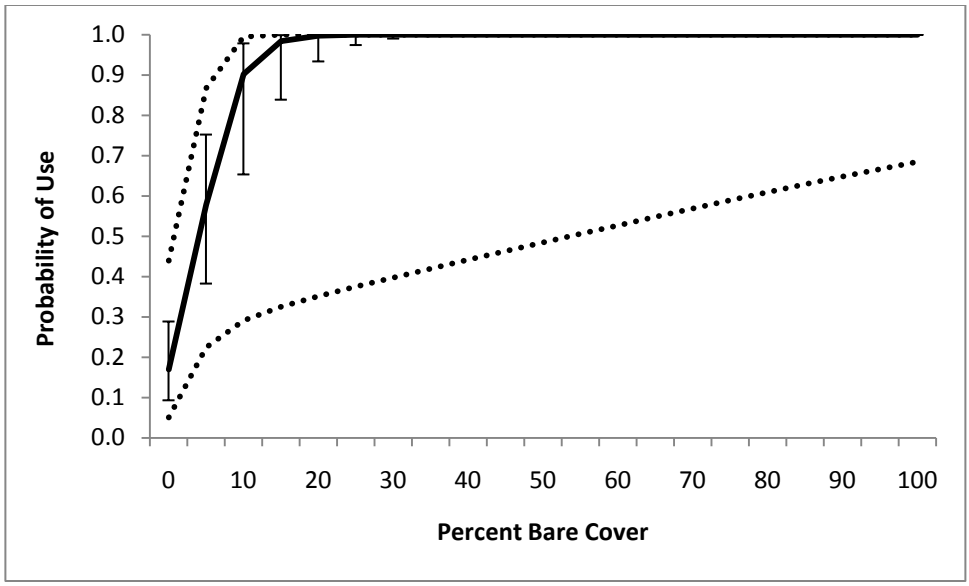
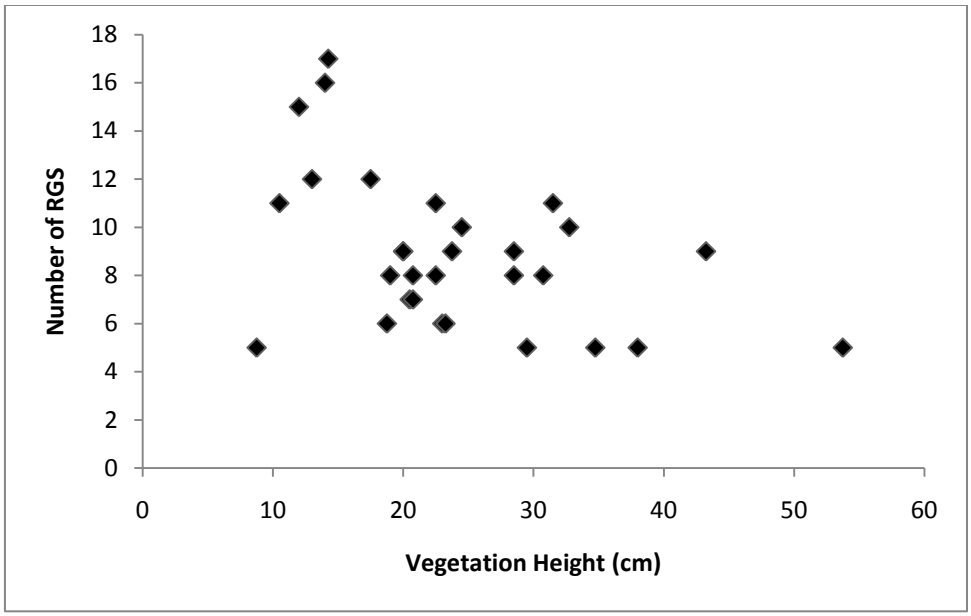


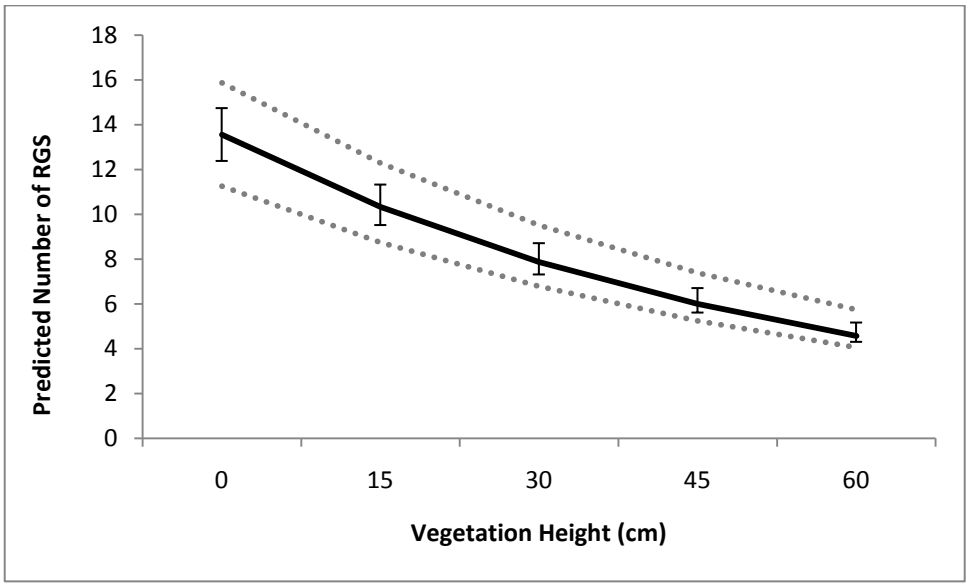
Figure 13. Predicted probability (±SE) (solid line), with 95% confidence intervals (dashed lines), of habitat use by Richardson's ground squirrels with varying amounts of bare ground, based on data from 2012 colony surveys.

3.2.4 Colony surveys: Abundance

RGS abundance at colony locations was best explained by vegetation height (Table 2), with this variable having a negative effect on abundance. Observed RGS abundance and the predicted number of RGS both decreased with an increase in vegetation height (Figure 14). The largest decrease in predicted RGS abundance (24%) occurred between 0 and 15 cm, followed by a further decrease of 18% as vegetation height increased from 15 cm to 30 cm. The largest colony (with 47 RGS) had an unbalanced influence on the modeling results for colony abundance data (Cook's distance > 4/n). Therefore, this location was removed from the dataset prior to this analysis.



(a)



(b)

Figure 14. Richardson's ground squirrel (RGS) abundance (±SE) at varying vegetation heights: (a) observed at used sites and (b) model predicted (solid line) with 95% confidence intervals (dashed lines). Data are from 2012 colony surveys.

4. DISCUSSION

4.1 General Discussion

I found that RGS presence and abundance was not evenly distributed across the landscape. There were large tracts of the landscape I surveyed where RGS were not found, and abundance was variable across the core area of their range. Variable presence and abundance across the study area is potentially indicative of large-scale processes affecting their greater distribution. Factors at the landscape scale such as climatic features (e.g., precipitation) or large scale environmental variables (e.g., geology) may be affecting this pattern. For example, RGS presence and abundance was highest in the Mixed Grassland ecoregion, which is differentiated from other ecoregions by soil type, temperature, and precipitation. Proulx et al. (2012) found that RGS were more abundant in the Brown soil zone in Saskatchewan, which is a feature that separates the Mixed Grassland ecoregion from the others. Previous research has also documented relationships between substrate, moisture, and the presence of other ground squirrel species (Yensen and Sherman 2003; Ball et al. 2005; Barker and Derocher 2010). Environmental influences on RGS presence and abundance are thus important considerations for management and conservation planning.

The current distribution and abundance of RGS based on my data indicates that population numbers are low relative to human perception. Many studies on RGS focus on pest management and the use of poisons (Goulet and Sadlier 1974;

Matschke and Fagerstone 1984; Ramsey and Wilson 2000; Proulx and Walsh 2007; Ling et al. 2009; Proulx and MacKenzie 2009; Proulx et al. 2009; 2010; 2011), highlighting the perceived importance of reducing the population of this species. For example, use of liquid strychnine (a RGS rodenticide) was banned in 1993 until 2007 when Saskatchewan approved the chemical for emergency use only; this continued until 2012 when the product was approved for non-emergency use across the Canadian prairie provinces (Wilk and Hartley 2008; Wilkins 2012). The lifting of this ban, in the face of documented collateral damage to non-target species caused by strychnine use, indicates that RGS are perceived to be over-abundant across their range in Canada. My broad-scale surveys revealed that only a small percentage (8%) of sites across the core of their range are even occupied. In addition, despite RGS populations recently being described as having reached epidemic levels (Proulx 2010), I found abundance at the broad scale to be consistently low, averaging only 3 RGS per used site. The average number of RGS found also represented the 75th percentile of the abundance data; thus, the majority of counts at occupied sites was actually less than 3. The average density of squirrels counted at used locations in my study (less than 1 RGS/ha) was more than 32-fold less than for a study that took place over a smaller portion of the same area from 2007 to 2009 (Proulx 2011). This difference between studies is important for two reasons: (1) it highlights the need to understand factors that affect RGS population sizes over both space and time; and (2) it emphasizes that current opinions about RGS abundance conflict with the actual state of the population at the landscape scale.

My targeted colony searches also revealed that RGS abundances were lower than expected. Due to the low numbers of RGS found from the broad-scale surveys, I specifically set out to find locations with high abundance. Although colony surveys were selected to have a higher average abundance than the broad-scale surveys, RGS abundance was still less than expected based on the reputation of the study area as being one of the most overpopulated regions in Saskatchewan. Even though abundances were 3-fold higher in colonies compared to broad-scale surveys, the density (2.5 ± 0.2 RGS/ha) was still much lower than most reports in the literature. For example, from 2007-2009 RGS densities averaged 32.1/ha with a maximum of 63/ha in an area of southwest Saskatchewan (Proulx 2011); and in southern Alberta Michener (2004) documented 109 adult females/ha with an average of 43.3/ha over a 15 year period. RGS densities in the literature are variable with recorded densities ranging from 5 to 124/ha (Howell 1938; Goulet and Sadlier 1974; Michener and Michener 1977; Michener 1979a; Michener and McLean 1996; Proulx and Walsh 2007, Proulx et al. 2009). The variability in RGS densities across space and time reinforces the need for consistent monitoring programs as the basis for determining appropriate management actions, and if any are even necessary.

Plant biomass removal by RGS at the densities observed in this study is likely to be negligible. The average mass of an adult squirrel is about 328 g, taking into account the average mass of adult male and female RGS, averaging their mass from hibernation emergence to immergence, and accounting for a 3:1 female to male ratio (Nellis 1969; Sheppard 1972; Michener and Michener 1977; Michener and Koeppl 1985; Michener 1989). Based on calculations of RGS consumption of

13 g/day food per 100 g body mass (Hansen and Reed 1969), and estimating a 4 month active period (Clark 1970; Michener and Koeppl 1985), an adult squirrel consumes approximately 5,125 g per year. From calculated yields of crop and hay, the average output in a season is approximately 9,100 kg/ha (Kowalenko and Summach 2001; Hansen and Schjoerring 2003; Malhi et al. 2007). Thus, the consumption per RGS would equate to 0.06% of the vegetative biomass produced in one hectare. Despite higher densities of RGS found during colony surveys, the potential agricultural damage inflicted would still affect less than 1% of the biomass produced per hectare. The importance of determining actual damage on a per squirrel basis and comparisons with economic thresholds would allow for identification of tolerable and intolerable levels of RGS. If RGS presence and abundance do not increase significantly from the levels I found during this study (or continue to decrease) my data suggest that poisoning is not necessary and may be detrimental to the persistence of this species.

There could be several explanations as to why the abundances were lower than expected based on other reported values. Other studies estimating RGS abundance are not based on attempts to survey a range of their distribution but were designed to address different research questions. Therefore, other studies would most likely be conducted at established colonies known to be relatively large and persistent. There are no previous estimates of population numbers that cover my study area; however, the low RGS presence and abundance from our surveys could be a residual effect of the extreme weather events in 2010 and 2011 in terms of high precipitation and flooding. Drought years have been associated with high RGS

densities, while wet years lead to increased mortality (Proulx 2010; 2012). Proulx (2012) documented a 30% reduction in a marked RGS population following heavy rains over a 9-day period in 2010. High spring precipitation has also been related to increased mortality in other ground squirrel species, such as Belding's (*Urocitellus beldingi*) (Morton and Sherman 1978) and Columbian (*Urocitellus columbianus*) (Neuhaus et al. 1999) ground squirrels. This emphasizes the need for information on how climate influences RGS populations in terms of their distribution and abundance, particularly if extreme weather events become more common.

Habitat selection by RGS is occurring across their range, and RSF modeling revealed that vegetative characteristics are important. In particular, vegetation height was a top predictor in three of the four analyses. It was included in top models for both the colony and broad-scale survey analyses, as well as in models of used versus unused locations and abundance. In general, the predicted number of RGS decreased as vegetation height increased; however, the probability of habitat use decreased dramatically at vegetation heights of 15 - 30 cm, levelling off to probabilities near zero at around 60 cm. This result is consistent with other studies. For example, Proulx et al. (2012) found higher RGS abundance in areas with vegetation height < 15 cm. Downey et al. (2006) also found vegetation height ≤ 30 cm was selected for by RGS and > 30 cm was selected against, although vegetation height was not measured precisely.

The apparent strong selection for low vegetation height by RGS may be explained in two different ways. First, higher vegetation heights may decrease the ability of RGS to visually scan for predators and increase areas for predators to take

cover, thereby increasing the risk of predation (Downey et al. 2006). This same mechanism may also explain why RGS were negatively associated with trees and shrubs, while positively associated with bare ground and tilled crops. Alternatively, RGS may be reducing vegetation height and increasing bare ground through their own grazing and burrowing activities, essentially creating the habitat that they 'select'. My data do not enable a clear distinction between these two possible explanations. However, given the low densities of RGS in our study, it seems rather unlikely that they affected vegetation height to any large degree. The fact that the location with the highest number of RGS (47) did not correspond with the highest percentage of bare ground (50%), supports this. Also, the idea that RGS are not selecting for lower vegetation heights, but it is a product of their foraging, does not explain the importance of trees and shrubs as predictors. RGS make up a large portion of the diet of many prairie species; thus predation most likely has a significant impact on RGS populations (Luttich et al. 1970; Michener 1977a; Schmutz and Hungle 1989; Schmutz et al. 2001; Michener 2004). If the predation risk explanation is correct, my data suggest that enhancing conditions for predator populations and higher vegetation would have a considerable impact on controlling RGS numbers.

RGS were positively associated with the amount of grass cover in survey plots. Interestingly, although RGS are considered a significant crop pest, the percentage cover of crop was not a strong predictor of RGS presence or abundance. Percentage of grass cover was a top predictor differentiating used versus unused locations from the broad-scale surveys and percent cover of grass was negatively

correlated with the percent cover of crop. This provides evidence that RGS select against areas with annual crops in favour of locations with high amounts of grass. Downey et al. (2006) also found that crops were selected against, and native pasture was selected for, when compared to availability. Other studies, although not directly measured, have indicated a preference of RGS for pastures and avoidance of cultivated areas (Yeaton 1972; Schmutz 1989). Although RGS were more likely to be present in grass-dominated areas, their abundance was higher in human-altered areas. The highest abundances were in tilled crops, followed by tame pasture, stubble, and hay crops. Thus, although RGS are not necessarily selecting for crop fields on the landscape scale, their abundance increases considerably when they are present in areas with these land use types. This could be because agricultural regions coincide with the most fertile soils and increase the availability of food to RGS. Also, pest control in these human-altered areas is most likely reducing the abundance of predators which indirectly reduces pressure on RGS populations. The fact that RGS are not selecting for crop fields, but are present in higher abundances is evidence that there needs to be a new, long-term strategy for pest management. In particular, we need to understand how crop fields are colonized by RGS and what attracts them to determine preventative measures.

The burrowing and semi-fossorial nature of RGS most likely plays a role in their habitat selection. RGS abundance increased as soil texture became finer. Fine soils are characterized as having higher clay content. This higher clay content could result in increased burrow stability as clay soils are more compact while sandy soils are looser (Reichman and Smith 1990). Clay soils provide more stable hibernacula

in other species (e.g., snakes; Watsell and Mackessy 2011), and are positively associated with burrow length, depth, and complexity in other ground squirrel species (Laundre and Reynolds 1993). The necessity for RGS to burrow, along with the fact that they do not need to drink water directly, would also explain the negative influence of water on RGS abundance. Large amounts of standing water would reduce the area in which burrows could be dug and would increase the risk of burrows being flooded. The importance of large-scale environmental factors such as soil and water processes on RGS distributions emphasizes the necessity to monitor populations at large scales.

Survey methods for RGS are not well developed and have never been used for such a large scale, most likely because this species is assumed to be over-abundant across its range. Road surveys are often used for monitoring wildlife populations because they are logistically efficient in terms of labour, accessibility, and the potential to survey large areas. Although biases in road surveys have been suggested due to evidence that roads can affect the distributions of particular species (Bellamy et al. 2000; Steen and Smith 2006; Rytwinski and Fahrig 2007; Andrews et al. 2008), recent research comparing model predictions from roadside sampling to off-road samples has shown that road surveys provide an accurate representation of species distributions, permitted that unpaved roads are also surveyed (McCarthy et al 2012). There was no evidence that road mortality may have skewed my results, and the inclusion of the call-playback method substantially increases the probability of detecting RGS (Downey et al. 2006). The systematic nature in which my data were collected on both paved and unpaved roads, as well

as not performing surveys during large fluctuations in RGS populations, is likely to have accurately captured the variability in the distribution of RGS across my study area.

4.2 Conservation and Management Implications

Many variables affect the abundance of RGS at a broad-scale. Therefore, an integrated pest management strategy that involves many different control measures would be most effective. It is necessary to implement preventative measures that will be successful over the long-term rather than the short-term reactionary methods that are used currently (e.g., poisoning). Along with traditional methods, ecology-based methods such as habitat modification should be integrated into RGS management. This would mitigate the extent to which current control methods negatively impact the environment. If RGS presence and abundance don't increase significantly from the levels I found during this study, or continue to decrease, my data suggest that poisoning is not necessary and may be detrimental to the persistence of this species making habitat modification the best management technique. Vegetation height was a strong predictor of RGS presence and abundance. A way to discourage RGS populations would be to keep vegetation height above 30 cm if possible, but at least above 15 cm. This could be achieved by ensuring that pasture and forage fields are not overgrazed, or by cutting vegetation (e.g., hay fields) to heights that discourage RGS occupancy. The opposite methods (i.e., decrease vegetation height to ≤ 15 cm) could be used to increase RGS

populations for conservation of SAR such as burrowing owls and ferruginous hawks. Other methods to aid both conservation and pest management would be to install shelter belts to increase proximity to trees and shrubs, reduce predator control, or install predator nest boxes/poles (e.g., ferruginous hawk poles). Encouraging predator populations via increased refugia and decreased control will enable natural population control while at the same time increasing biodiversity and reducing negative environmental effects.

4.3 Future Research

Long term, large-scale monitoring programs focused on RGS would provide data needed to determine best management practices. Future research that incorporates different control methods and grazing regimes with RGS distribution would be beneficial to understanding how land practices affect RGS populations. Comparing trends in rodenticide use with RGS and RGS predator distributions, along with a greater understanding of predator-prey dynamics is also critical for effective preventative management practices. Information is needed to determine the specific role that RGS play in abiotic processes and vegetative structure. To that effect, research on the relationships between RGS and other grazers is needed to determine the level at which RGS compete with livestock for forage or if RGS are actually increasing the nutritional quality of vegetation available to other grazers. The distribution of SAR and estimates of biodiversity should be compared with RGS distribution. This information is essential to broaden our understanding of

RGS ecology and their importance to the ecosystem. Lastly, economic impacts in terms of RGS damage and cost of RGS control are vital to our assessment of management strategies and what actions are necessary versus excessive.

5. CONCLUSIONS

I hypothesized that RGS abundance and distribution would be variable across the landscape and be influenced by extrinsic factors. I predicted that habitat features such as local land use, land cover, soil texture, and vegetation height influence RGS presence and density. My specific objectives were to: 1) Determine how RGS are distributed, in terms of presence and abundance, across a broad scale at the core of the RGS species range; 2) Determine if habitat selection by RGS is occurring and, if so, which predictors best differentiate locations used by RGS and unused locations; and 3) Determine if there is a relationship between environmental variables and RGS abundance at locations where RGS are present, and which predictors have the strongest influence on RGS abundance.

I mapped how RGS are distributed in terms of presence and abundance from data that I collected using road surveys and alarm call-playbacks across a broad scale at the core of the RGS species range. I found that RGS presence and abundance was not distributed evenly across the study area and I found lower than expected numbers of RGS in terms of both presence and abundance. I also identified colony locations in an area known to have high numbers of RGS and determined abundances to be lower than expected based on the reputation of the area. I determined that habitat selection by RGS is occurring and that vegetation and land cover variables best differentiate locations used by RGS and unused locations. Lastly, I determined that RGS abundance is influenced by many

environmental features at the landscape scale but that vegetation height alone has the strongest influence on RGS abundance at colony locations.

The information from this study provides a useful first step toward understanding the factors that affect the distribution and abundance of RGS by identifying habitat features that are selected by this species. RGS have been largely overlooked from the habitat research perspective despite the dominant role they play in prairie ecology. The fact that they are agricultural pests, yet also responsible for the persistence of SAR, necessitates research to acquire more detailed information on their distribution, density, and habitat requirements. My research demonstrates the utility of implementing RGS surveys to determine the habitat selection of this species across a large range in a multi-use habitat. Consistent monitoring programs should be implemented for this species to develop sustainable management and conservation practices based on predicted distributions and habitat associations.

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