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Population, individual and behavioural approaches to understanding the implications of habitat change for arctic ground squirrels

by

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Abstract

The ecological niche describes the entire set of resources and environmental conditions suitable for species to occur and persist. In northern ecosystems, rapid climate change appears to be altering these conditions and increasing the likelihood of shifts in distribution and abundance of species, with unknown consequences for resilience of ecosystem processes. Arctic ground squirrels are a widespread northern species, acting as agents of community disturbance and prey for many northern predators. Understanding the effects of habitat characteristics on occurrence and population persistence of arctic ground squirrels will improve projections of how habitat change may affect their ecosystem role. I compared arctic ground squirrels inhabiting an alpine ecotone extending across shrub, shrub-tundra and tundra habitats in southwest Yukon, and considered a variety of ecological factors determining distribution, population dynamics and individual behaviour.

Populations in high suitability habitats (tundra) have greater viability and persisted at higher density with greater survival compared with low suitability habitats (more shrubs), possibly driven by a reduced risk of predation associated with lack of visual obstruction. Surprisingly, intermediate levels of shrub cover appeared to support the lowest densities and lowest survival in adult females. The apparent low suitability of shrub-tundra was also characterized by temporary habitat associations by non-resident individuals.

Trends in behaviour and individual condition between habitats were inconsistent with those observed at the population level. These patterns resulted from either differences in individual state between habitats, or possibly maladaptive behaviours in transitional shrub-tundra habitat. Specifically, giving-up densities, which indicate costs of foraging and individual condition, were not consistent with predictions based on the observed population processes. Individuals in shrub habitat had higher giving-up-densities, lower adult female mass, and lower juvenile growth rates compared with shrub-tundra. Other factors showed no clear association with density or apparent habitat suitability, including reproductive output and juvenile coccidial parasite load.

In general, the increasing occurrence of dense shrub in the Arctic is likely to reduce the density and restrict the distribution of arctic ground squirrels. If these low suitability habitats become more isolated, the potential for local extinction of arctic ground squirrel populations may increase.

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Chapter 1

The effect of shrubs on habitat suitability of Arctic ground squirrel across an alpine ecotone

The distribution and density of many species are being affected by habitat changes caused by anthropogenic activities (IUCN 2010) and habitat change is increasing extinction risk of species globally (Thomas et al. 2004). To develop a better understanding of current distribution and population dynamics across heterogeneous landscapes and more accurately project responses to change, it is necessary to quantify the ecological niche of a species. However, the ecological niche is a complex multidimensional construct describing the resources and environmental conditions necessary for species occurrence (Hutchinson 1957) and may be difficult to fully parameterise. Even if the niche could be fully quantified, this alone may provide insufficient information to assess likelihood of persistence of populations in different areas. In addition, as individuals adapt to prevailing conditions a species' niche may become altered. Projection may then rely upon integration of plastic and adaptive responses to environmental change.

Prior to Hutchinson's popularisation of the niche concept, two components of a species' niche were identified. The Grinellian niche (Grinnell 1917), encompasses the environmental factors necessary for positive population growth. In contrast, the Eltonian niche (Elton 1927) emphasises interactions with other species, and population persistence in the presence of these interactions (Hirzel and Le Lay 2008). Hutchinson recognised that species do not exist across all areas defined by the fundamental niche and introduced the concept of the realised niche to describe the subset of conditions where individuals are found.

Recently, ecological niche modelling has been a popular means of assessing current habitat suitability and also for projecting responses to change. In order to project species responses to changing climate and extend projections beyond those based on association rather than mechanism (Pearson and Dawson 2003), an understanding of the responses of species to changing biotic environments must be developed. This requires an assessment of the patterns and causes of individual and population responses to habitat suitability.

Although there are several differing definitions of ecological niche, habitat suitability and habitat quality, none apply perfectly in all contexts. Hirzel and LeLay (2008) suggested that the ecological niche refers to environmental factors affecting fitness, while habitat suitability refers to those affecting occurrence. However, much of the development of ideas concerning the density of populations and fitness of individuals across different habitats also uses the term habitat suitability (e.g. Fretwell 1972). High individual fitness does not always scale to viable populations, this is particularly true given the effects of density dependence on fitness in high density populations (Fig. 1.1). The concept of niche is also ambiguous with respect to distribution; in some cases (such as source-sink systems) components of the realised niche may exist outside the fundamental niche (Sillero 2011). This highlights the difficultly not only in quantifying ecological niche but also in ascertaining the relationship between ecological niche and processes at the individual, population and species level.

Ultimately, perhaps quantifying the ability for populations to establish and persist across heterogeneous environments is the ultimate aim of many studies in this field. Holt (2009) referred to both the establishment and persistence niche being important. I therefore use habitat suitability to refer to the potential for a population to establish and persist in a given habitat. I use individual and population level studies to assess habitat suitability across heterogeneous environments. I also consider the relative utility of population and individual-based perspectives when assessing habitat suitability.

Fretwell (1972) proposed conceptual models to describe trends in fitness and survival across habitats varying in suitability; many more recent models are still grounded in this theory (Kacelnik et al. 1992; Křivan et al. 2008). The ideal-free distribution (IFD) proposes that individuals will be distributed to maximize their fitness according to habitat suitability. Under this model higher suitability habitats support higher densities, but fitness of individuals should be equal between habitats. The ideal despotic distribution (IDD) was developed as an extension to the IFD, where territoriality of dominant individuals causes habitat suitability in a given area to be lower for less dominant individuals. Territoriality is assumed to be density dependent and higher at greater densities; therefore territoriality is greatest in high suitability habitats. Under the IDD, higher suitability habitats promote both higher survival and higher population densities.

The ideal free and ideal despotic distributions provide a link between population processes and the individual by linking individual fitness to density within constituents of a metapopulation. Although fitness may be comprised of survival and lifetime reproductive success, studies elaborating on IFD and IDD models have often focussed on foraging and energy acquisition as a proxy for fitness (e.g. Kacelnik et al. 1992). While the IFD and IDD have been developed further since their conception

(Křivan et al. 2008), most equilibrium models still result in one of two predictions between the relationship between habitat suitability, individual fitness and density:

A. **Ideal-free:** Individuals in high suitability habitats have equal fitness to those in low suitability habitat, but high suitability habitat supports higher population densities.

B. **Ideal-despotic:** Individuals in high suitability habitats have greater fitness and populations exist at higher density.

A further set of predictions may emerge from non-equilibrium dynamics (Hansson 1996; Cassini 2011) including situations where individuals have imperfect information. One common non-equilibrium result may be that high density occurs as a result of high survival in habitats that confer higher fitness (Hansson 1996). Although this does not require equilibrium, this pattern is indistinguishable from prediction B and is therefore considered a non-equilibrium mechanism with the same emergent properties.

Ecological and perceptual traps are instances where poor suitability habitats may be colonised by individuals in good condition and can have high densities, however once in these habitats individuals should be expected to have low fitness (Kokko and Sutherland 2001; Patten and Kelly 2010). This leads to the final prediction:

C. Density in low suitability habitat is equal or higher than that in high suitability habitat, however survival in low suitability habitat is greatly reduced.

In this thesis I assess the relationship between habitat suitability and population dynamics (survival, density and reproductive output), individual condition (mass, growth rates and parasite load) and foraging behaviour for herbivores foraging under predation risk. Two important niche components for herbivores are the conditions that determine local plant community and the activity of predators. One component affecting habitat suitability which is poorly categorised by the traditional view of the niche is the way in which environmental factors can alter species interactions and thereby affect persistence, for example how landscape structure affects predation risk. In this thesis, I consider these three components of the niche to address the following questions

1. What are the ecological factors that determine habitat suitability for arctic ground squirrels?
2. What models best represent distribution of individuals within a metapopulation where habitats vary in suitability?
3. Do inferences from behavioural indices of habitat suitability correlate well with those derived at the population level?
4. What are the relative roles of density and habitat suitability in determining individual condition?

Context

The Arctic has and will continue to experience major environmental changes associated with climate warming (ACIA 2005; AMAP 2011). Recent studies have demonstrated effects of climate change on northern wildlife (Hansen et al. 2011; Kutz et al. 2005) and predictions suggest warming will have major effects on arctic wildlife (Jensen et al. 2007; Durner et al. 2009; Freitas et al. 2008). Most effects of warming upon species appear to be mediated through changes in the cryosphere, habitat structure and species interactions, rather than occurring as direct effects of climate.

Dominant arctic small mammal species in the Arctic appear to have become more restricted in distribution with long-term warming since the last glacial maximum (Prost et al. 2010; Zazula et al. 2011) and are likely to be vulnerable to future warming. These species form a major component of arctic food webs (e.g. Krebs 2010) and have a major role as agents of disturbance via burrowing (Price 1971); alterations to their density and distribution could have substantial effects on animal and plant communities in the Arctic.

Arctic ground squirrels are a widespread species with Holarctic distribution; they live in colonies that can reach very high densities and have a significant ecosystem role as prey species and agents of disturbance. Arctic ground squirrels may be affected by habitat change, cryospheric change and direct effects of climate. In this thesis, I review the potential effects of climate change upon arctic ground squirrels across their entire range via both direct effects of climate and those mediated through biotic and other abiotic interactions. I then examine the likely effects of habitat change occurring toward the southern and lower altitude limits. In order to do this, I assess what determines habitat suitability across a shrub to tundra ecotone and variation in population processes, individual condition and behaviour associated with these habitats varying in shrub density.

Implications of shrub encroachment for arctic ground squirrels

Across the Arctic, the distribution and density of canopy-forming shrubs are changing (Sturm et al. 2001; Tape et al. 2006). Willow (*Salix spp*), dwarf birch (*Betula nana*) and green alder (*Alnus crispa*) are the three major shrub types in northern and alpine ecosystems that have shaped ideas about shrub encroachment in northern ecosystems (Sturm, Racine and Tape 2001), or ‘shrubification’ (Myers-Smith et al. 2011). The most common observed response of shrubs to warming has been increases in local density (Tape et al. 2006; Myers-Smith et al. 2011; Naito and Cairns 2011). In addition, the latitudinal and altitudinal limits of shrub distribution appear to be increasing northwards and to higher elevations. Many processes associated with warming may promote range expansion and density increases of shrubs in the north. Warming temperatures have been associated with increased productivity in the north and increases in shrubs in the arctic have been associated with direct effects of increased temperature, increased nitrogen, disturbance from permafrost degradation and increased moisture (Lantz et al. 2009; Myers-Smith et al. 2011; Naito and Cairns 2011), however, the dominant mechanisms of expansion are not well resolved.

Shrub encroachment is likely to occur into many arctic ground squirrel habitats, and has the potential to affect distribution and density in multiple ways. Changes in the structure of the landscape may alter predation risk via decreased ability of squirrels to detect predators or, conversely, decreased ability of predators to detect prey. Predation risk may also be affected by the ability of individuals to escape in a landscape with more physical obstructions (Schooley et al. 1996). Changes in plant species composition could also alter forage availability and quality. Finally, shrubs can facilitate drainage, creating more favourable areas for burrowing.

Predation risk

The relationship between visibility and predation risk has been shown to differ for different prey species. For some species, taller vegetation confers disadvantages by reducing detectability of predators, while for other species, advantages accrue from increasing the cover in which to evade predators. In some circumstances, taller vegetation can also reduce the efficacy of predator attack (Pietrek et al. 2009). In many cases, a combination of these factors will determine the behaviour and success of prey species in an environment (Hannon et al. 2006).

Reduced visibility as a result of increased shrub cover could either affect arctic ground squirrels directly, by influencing predation mortality, or more indirectly as a result of changes in time and energy allocation to predator-sensitive behaviour. Predator-sensitive behaviour can affect population dynamics via changes in condition associated with increased time allocation to predator-sensitive behaviours (Hik 1995; Sinclair and Arcese 1995).

An increase in predator sensitivity in response to increased visual obstruction has been observed in many species (e.g. Lagory 1986; Martella et al. 1995). In ground squirrels and other sciurids, visual obstructions have been widely shown to increase vigilance both experimentally and associated with variation in vegetation height (Arenz and Leger 1997; Bednekoff and Blumstein 2009; Mateo 2007; Sharpe and Horne 1998). Increased investment in vigilance can reduce the time individuals spend foraging (Mateo 2007) and can have negative effects on condition and long-term survival.

Conversely, woody canopy-forming species may provide important cover and reduce predation risk. Shrubs differ from taller herbaceous species in that they provide overhead cover in addition to lateral cover. Many raptors have been known to forage preferentially on areas of low vegetative cover (Aschwanden et al. 2005; Bechard 1982; Malan and Crowe 1997). Overhead cover may convey advantages for prey by providing cover from avian attack and reducing prey detectability to predators which may gain advantages from a more elevated eye line than small prey species. In the degus *(Octodon degus)*, increases in vigilance were greater in response to lateral visual obstruction imposed by herbaceous cover than that imposed by shrub, most likely due to these differences in risk associated with the two types of cover (Ebensperger and Hurtado 2005). Costs and benefits of shrub cover have been complex in other species of ground squirrel and are dependent on the specific form of cover (Hannon et al. 2006).

Arctic ground squirrels appear to rely heavily on visibility for predator detection. Vigilance and calling are very conspicuous features of ground squirrel behaviour. In the boreal forest, where visibility is lower than in tundra, individuals show a preference for burrow site locations with a less obscured view (Karels and Boonstra 1999). Boreal forest populations appear to be sink populations with insufficient population growth to persist in the absence of immigration, in comparison, tundra appears to act as a population source (Gillis et al. 2005; Donker and Krebs 2011). These differences between habitats have been attributed to variation in predation risk; however, fine scale comparisons between more similar shrub and tundra habitats have not been made. More complex responses to visibility may be identifiable between these proximal habitats given predator assemblages will be similar and differences in visibility are not accompanied by major differences in forage species.

Forage availability and quality

Shrub encroachment will not only expand the distribution and increase the density of shrubs, but also can be expected to affect plant communities under the shrub canopy. Increased shrub cover has been associated with increased forb cover and decreases in graminoids, dwarf shrubs, bryophytes and lichen (Pajunen et al. 2011). Arctic ground squirrels are generalist foragers and specific information on diet is limited to a single location, however, forbs and seeds appear to be major diet constituents. In July and August, the combined percentage of stomach contents of deciduous and evergreen shrubs was less than 2%, suggesting shrub are not a preferred diet constituent (Batzli and Sobaski 1980). Increased forbs under shrub canopies could be beneficial for arctic ground squirrels, however these changes may occur at the expense of fewer seeds from graminoids and associated fatty acids necessary for hibernation. The northern Idaho ground squirrel (*Urocitellus brunneus brunneus*) has undergone considerable decline in recent years and is listed as endangered by the IUCN (van Horne 2007). This has been attributed to changes in forage due in part to fire suppression and resulting conifer and shrub encroachment reducing availability of seeds as well as changes in phenology associated with changes in community composition (Sherman and Runge 2002).

Changes in community composition could therefore affect arctic ground squirrels; however, within the forb functional group, there is considerable variation in preference between species, with particular preference for *Lupinus arcticus, Astragalus alpinus* and *Pedicularis capitata* (Batzli and Sobaski 1980). *Lupinus arcticus, Astragalus alpinus* are legumes which may be particularly preferred forage. Responses are likely to depend more on whether preferred species become more abundant rather than changes at the level of the functional group. In addition arctic ground squirrels may be more limited by foraging time than forage availability given their broad diet.

Drainage

Arctic ground squirrel burrows are limited to microhabitats with sufficient soil drainage (Carl 1971; Batzli and Sobaski 1980). In wet habitat with little topography, excessive moisture may limit distribution of arctic ground squirrels or limit colonies to a few drier microhabitats. Encroachment of canopy forming shrubs may aid drainage of soil, increase the area suitable for burrowing and allow for expansion of arctic ground squirrel distribution or increases in density.

Objectives, study site and design

Part 1: The role of arctic ground squirrels in northern ecosystems and potential effects of climatic stressors on future density and distribution

In the first part of this thesis I provide a review of the past and present ecology of arctic ground squirrels and discuss current and future pressures facing this species associated with climate change.

Chapter 2: *Arctic ground squirrels (Urocitellus parryii) as a driver and indicator of change in northern ecosystems.*

Given arctic ground squirrels occur over a wide range of habitats over a broad geographic distribution, predominant climatic stressors are likely to vary across their distribution. In this chapter, I assessed potential impacts of climatic stressors across the entirety of their range. I also introduced the basic biology of arctic ground squirrels and key factors determining density and distribution. From these analyses I assessed the implications of change in arctic ground squirrel distribution and density for ecosystems processes in the north,

Part 2: Variation in arctic ground squirrel behaviour and population dynamics associated with shrub cover: Implications of shrub encroachment for future distribution and density

In the second part of the thesis I considered the process of shrub encroachment, which although widespread, is likely to have greatest initial impact at the more southerly and lower altitudinal extents of the current distribution. I assessed the potential effects of shrub encroachment upon arctic ground squirrel population dynamics and behaviour. Using variation in shrub density across an altitudinal gradient, I considered responses of arctic ground squirrel populations and individuals to different levels of shrub cover. From these data I assessed the implications for habitat suitability under increased shrub density. I also evaluated the relative value of different indicators of habitat suitability gleaned from population processes, individual animals and behavioural observations.

Study species

Arctic ground squirrels are a Holarctic species, distributed throughout northern North America and eastern Siberia (Helgen et al. 2009). They are a colonial rodent reaching approximately 1kg in mass (Buck and Barnes 1999, Fig. 1.2) and occupy a wide range of habitats including arctic and alpine tundra, shrub-tundra and boreal forest (e.g. Carl 1971; Gillis et al. 2005; Donker and Krebs 2011). Arctic ground squirrels live colonially in often extensive burrow systems (Carl 1971, Fig. 1.3). Life history is entrained around a long hibernation period (7-8 months, Buck and Barnes 1999). Squirrels emerge from hibernation between mid-March and late-April, with adults males emerging first and yearling latest (Sheriff et al. 2011). Breeding occurs after female emergence and is followed by an approximately 25 day gestation period, after which juveniles spend another ~28 days in burrows prior to emergence (Byrom and Krebs 1999). During the active season, sufficient mass gain is important to increase overwinter survival probability and individuals gain considerable mass during the active season (Buck and Barnes 1999).

Study site

This study was conducted in an alpine valley in the Ruby ranges, SW Yukon Territory (61.2147 N; 138.2798 W, Fig. 1.4). Arctic ground squirrels were studied across an elevational gradient from 1450m to 1950m above sea level (A.S.L.). Across this gradient plant community composition varied considerably, particularly in relation to canopy forming shrubs. The dominant canopy forming shrub species in the valley were three willow species (*Salix glauca, S. richardsonii* and *S. pulchra*). These species varied in both size and density across the ecotone. At the highest elevations, shrubs were rare and generally very short in stature reaching only about 20-30cm. At lower elevations, shrubs increased in density and height, forming large patches interspersed with open alpine tundra. At the lowest elevations, shrub formed an almost contiguous canopy and reached over a metre in height. This gradient allowed assessment of variation in behaviour and population dynamics across a wide range of visibilities associated with shrub cover within a small area; this minimised variation climate and predator community between sites such that much of the variation observed could be attributed to variation in vegetation rather than site specific differences in other variables.

Several alpine tundra vegetation communities were present across the study site, which was characterised by high levels of spatial hereogeneity. Tundra included *Dryas octopelata* and dwarf willow (*Salix reticulata, S. polaris, S. arctica*) dominated communities, *Cassiope* beds, graminoid dominated communities containing mainly *Carex* species and more mixed communities with graminoids interspersed with large with patches of forb species such as *Pedicites frigida* and occasional *Polygonum bistorta,* as well as those with large areas of moss and lichen. In addition, there were considerable areas of talus largely devoid of vegetation, where collared pika (*Ochotona collaris*) and hoary marmots (*Marmota caligata*) were common. Intermediate and lower elevations were characterised in some cases by increasing occurrence of patches of *Vaccinium* and *Epetrum* shrubs in addition to canopy forming willows, although spatial heterogeneity was also considerable at lower altitudes. Communities on exposed summits (~2000m A.S.L.) were lichen dominated and associated with a much greater proportion of exposed ground and bare rock, but were not included in this study.

Across this alpine valley, there was the potential for variation in visibility, forage and drainage associated with shrub cover. Differences in visibility were very marked between habitats, and reflected a transition from consistent long distance visibility at the highest altitudes to almost complete visual occlusion past 10m in dense shrub. Forage varied somewhat, particularly in terms of the availability of canopy forming shrub species, although at lower altitudes much of the foliar biomass of shrub may be relatively inaccessible due to shrub height. In addition, canopy forming willow-shrub does not appear to be a major constituent of arctic ground squirrel diet (Batzli and Sobaski 1980). Other species associated with shrub cover may vary between habitat types, however there is also high spatial variation within habitat types associated with high local heterogeneity. In general, available forage was probably most similar between shrub and transitional shrub-tundra habitats. Drainage was probably the least likely factor to show systematic variation associated with shrub cover. Although local variation in drainage and propensity for flooding was evident associated with topography and timings of local snowmelt, relative to flat arctic tundra, all habitats are relatively well drained as they occur on considerable slopes. Drainage may be important locally but probably has less influence than in non-mountainous areas. Given these trends I assessed the role of habitat type in determining habitat suitability in relation to site fidelity, population dynamics and predator sensitivity and the underlying causes of this variation.

Experimental design considerations and constraints

In Part 2 of this thesis, most analyses compare individuals and populations between three habitats: tundra, shrub-tundra and shrub. These habitats differ in plant species composition and structure, which influences visibility. In tundra, shrubs are infrequent and small in stature, therefore the main impediments to visibility are small scale topography and graminoid vegetation. In shrub habitat the dominant impediments to visibility are tall and dense shrub cover (canopy-forming willow species). Shrub-tundra represents a transitional habitat between shrub and tundra with intermittent patches of canopy-formatin shrubs interspersed with graminoid and forb dominated meadows. High spatial heterogeneity in vegetation height in shrub-tundra probably has the greatest influence on local visibility, and in this respect shrub-tundra is distinct from shrub or tundra.

My study area was constrained to a single 4 km^2 valley by operational logistics and in order to minimise additional sources of variation including local weather and predator densities. This approach placed some restrictions on spatial replication of each habitat, particularly for shrub-tundra. As a transitional habitat between shrub and tundra, shrub tundra was limited in spatial extent compared with tundra and shrub, and only a single 4ha site was included. I acknowledge this as a potential problem for some types of analysis, but several approaches were taken to minimize this limitation.

The problem of balancing replication with collecting large scale data has been widely discussed (Carpenter 1989; Hargrove and Pickering 1992; Schindler 1998). For example, Oksanen (2001) highlighted the perspective that selecting an appropriate spatial scale for ecological studies should always take precedence over replication, such that the ecological relevance of the spatial extent should not be sacrificed in order to increase replication. In this thesis, the requirement to limit spatial extent to minimise spatial variation in confounding factors, while having sites of sufficient area to portray population processes, separated by sufficient distance to prevent pseudoreplication constrained my study design. However, I also adopted an alternative approach by conducting an analysis using individual responses to visibility (see Appendix). While regression (as used in Appendix) is suitable in some cases, it does not allow for potential non-linear effects of visibility, which may occur as a result of the differing impediments to visibility in shrub and tundra and the complex trade-offs that determine net costs or benefits of visibility.

Increases in local density of shrub is the dominant process characterising this site and many other tundra communities (Myers-Smith 2011; Myer-Smith et al. 2011), and this process is well represented by the transition zone between shrub and shrub-tundra at my study site. The increase in the extent of shrub tundra habitat is one of the more imminent changes to be experienced by arctic ground squirrels (Wheeler and Hik 2012), and my experimental design allowed an exploration of these interactions and dynamics.

Chapter 3: *Comparison of emigration and transience models for estimating survival and identifying temporary habitat associations for a central-place forager, the arctic ground squirrel (Urocitellus parryii).*

The fidelity of individuals to a given area may provide important information about the suitability of that habitat. Individuals may have temporary associations with a habitat if they simply pass through a habitat and do not settle, or if they temporarily emigrate from a habitat. Temporary movements are often ignored when estimating survival and density, and may bias these estimates. To assess the extent of temporary movements I fitted models incorporating transience (short-term association with a habitat followed by permanent absence) and temporary emigration (short-term associations and short-term absences followed by return to a habitat). I predicted that there would be greater habitat fidelity in higher suitability habitats.

Chapter 4: *Arctic ground squirrel habitat suitability across a gradient of shrub tundra: contrasting assessments from population and behavioural models.*

Forecasting individual species responses to climate warming and subsequent vegetation change requires a clear understanding of suitability of different habitats. Habitat suitability is often measured at the population-level using density and survival estimates, or at the individual-level using behavioural decisions or individual condition indices. These two approaches are rarely integrated, and predictions of the two approaches may conflict. In this chapter I compared survival and density for populations of adult female arctic ground squirrels inhabiting tundra, shrub-tundra and shrub. I then assessed giving-up density in each habitat and temporal changes in female mass. These estimates were compared to assess habitat suitability and evaluate the drivers of differences in these indices.

Chapter 5: *Reproductive investment and juvenile health in relation to shrub cover: Assessing the relative roles of density and habitat suitability.*

Investment in reproduction and juvenile health can have substantial effects on population dynamics and population persistence. Effects of habitat suitability on reproductive output and juvenile health can also be affected by variation in local density. If populations in high-suitability habitat are large, density dependent effects may reduce investment in and condition of juveniles. I compared estimates of the number of juveniles emerging from natal burrows between habitats and reproductive output of females between habitats to assess the role of habitat versus density dependence in determining these trends. I then considered juvenile growth rates and health using an index of coccidial parasite load and compared these between habitats. The role of habitat suitability related to shrub cover and other factors was discussed as well as the importance of density dependence in these processes.

Chapter 6: *Giving up density, vigilance and alternate strategies to minimise predation risk across a shrub to alpine-tundra ecotone: Assessing the implications of shrub encroachment for foraging costs for arctic ground squirrels.*

In order to assess the role of predation risk in determining habitat suitability, I investigated predator sensitive behaviour and foraging costs across multiple scales, in shrub, shrub-tundra and tundra habitats occupied by arctic ground squirrels. Giving-up density, time allocation and temporal trends in vigilance were compared between habitats. Effects of local visibility within each habitat type were also compared between habitats. The relative roles of predation risk, individual state and missed opportunity cost in driving habitat related differences in behaviour were assessed. Time and energetic costs of foraging in each habitat were also compared.

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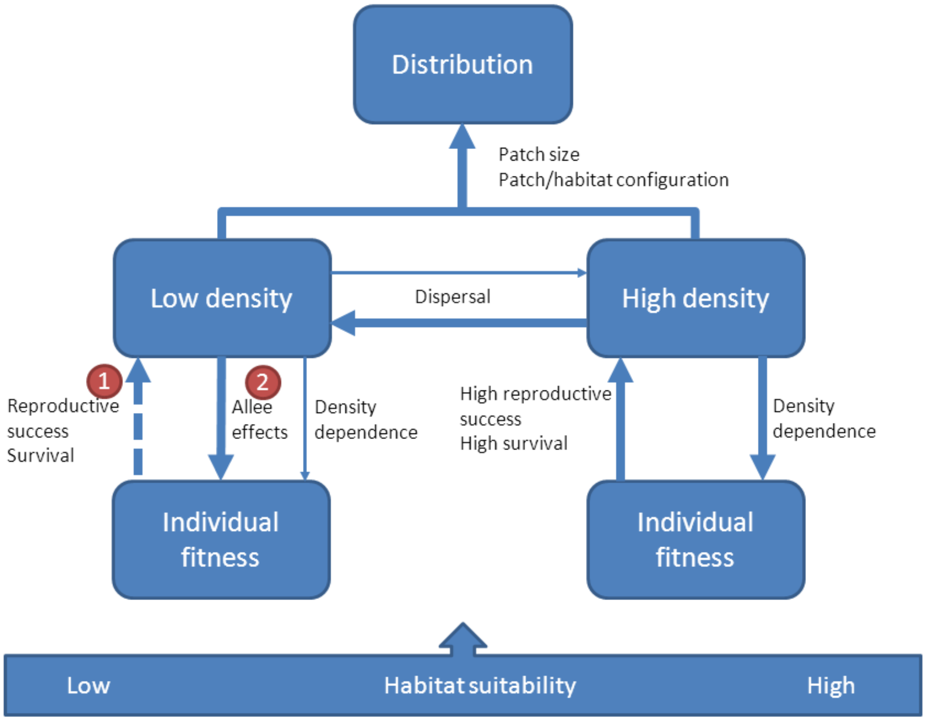

Figure 1.1. Representation of key relationships between individual fitness, population density and distribution with variation in habitat suitability. Arrow width denotes the potential strength of each effect. Broken arrows suggests effect is less certain. In low density populations in low suitability habitat (1) refers to the potential for reproductive success and survival to vary depending upon the relative effects of density and habitat suitability in determining fitness, (2) refers to the potential roles of Allee effects (Allee et al. 1949) at low density where fitness is reduced.

Figure 1.2. Adult arctic ground squirrels, (a) being vigilant from a burrow entrance; (b) collecting dried vegetation for bedding. Photo credit: Helen Wheeler.

Figure 1.3. Excavated soil and rock forms a mound around many arctic ground squirrel burrow systems, creating substantial local disturbance. Photo credit: Helen Wheeler.

Figure 1.4. Location of the study site showing part of the alpine valley, which extends to both higher and lower elevations between 1200 and 1900 m. Photo credit: Helen Wheeler.

Chapter 2

Arctic ground squirrels *(Urocitellus parryii)* as a driver and indicator of change in northern ecosystems[1]

Introduction

Climate change in the Arctic is occurring at some of the fastest rates globally, causing considerable biotic and abiotic disturbance across the entire region (ACIA 2005; Sturm et al. 2005; Gilg et al. 2009; Post et al. 2009; Prowse et al. 2009a). In addition to warming air temperatures, a reduction in sea ice, glaciers, icecaps, permafrost and snow cover have been observed (ACIA 2005; IPCC 2007). Climate forcing is also leading to significant increases in the variability of weather systems, and changes in seasonal phenology (IPCC 2007). As southern species shift their distributions northward, new predators, competitors, diseases and parasites are likely to follow (Patz et al. 2000; Harvell et al. 2002; Kutz et al. 2009; Higdon and Ferguson 2010; Davidson et al. 2011). Other social and economic activities, and the political systems under which they operate, will determine the extent to which these ecosystems are affected by oil and gas development, mineral exploration, tourism, habitat fragmentation, pollution and other disturbance (Forbes et al. 2004; Steward et al. 2005; Whiteman et al. 2004). These pressures may influence arctic species most at the margins of their northern, southern and elevational range limits.

While species distributions may expand further northwards as climatic warming increases suitability of some environments, range may be lost at southern limits. In

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addition, local development activity may also facilitate distribution change. Northern ecosystems may be particularly slow to recover and adjust to change because of species' low reproductive rates and slow growth typically associated with colder climates (Usher et al. 2005). In order to accurately assess and monitor ecosystem health, current information about species status is required over a range of different conditions.

Certain critical ecosystem components are sometimes overlooked in ecological research and monitoring programs. The most extensively studied mammal species with respect to climate change, conservation and northern ecology are large and charismatic (Simberloff 1998) or under high risk of extinction (Gaston and Fuller 2007). Large-bodied species with high metabolic needs and specific habitat requirements have the potential be good local indicators of ecosystem functioning (Simberloff 1998). However, many threatened species of current conservation interest often have, by virtue of their low abundance, limited impact upon the ecosystems they inhabit. Abundant, smaller-bodied species can have substantial effects on their habitats as ecosystem engineers or central components of food webs (Krebs 2011; Prugh and Brashares 2012). Such species may be particularly underrepresented in scientific literature compared to charismatic or endangered species.

Arctic ground squirrels *(Urocitellus parryii, nee Spermophilus parryii)* are a widely-distributed species reaching high local densities across the Arctic. They exert strong edaphic effects through burrowing (Price 1971), are an important prey species for many northern carnivores, and affect local vegetation composition (McKendrick et al. 1980). Arctic ground squirrels may facilitate and amplify ecosystem change, but have received relatively little attention with respect to basic ecology compared to other arctic species.

As a vocal and conspicuous species, they are easy to observe, from both their physical presence and burrowing activity. Simple, time and cost effective monitoring techniques can be used to observe trends in species density and distribution; these methods have been developed in work on this and other ground squirrel species (e.g. Downey et al. 2006; Wiewel et al. 2007; Barker and Derocher 2010). Arctic ground squirrels could prove to be useful ecological indicators of ongoing climate and ecological change.

I evaluated the evidence that arctic ground squirrels are ecosystem engineers and keystone species in arctic and alpine environments, their past and present distribution, and potential responses under projected climate change scenarios. Finally, I examined the extent of published literature about arctic ground squirrels and identified several areas where further understanding is necessary.

Study species

The arctic ground squirrel is a relatively small colonial mammal (adult peak mass up to 1kg, Buck and Barnes 1999b), which lives in burrow systems that are often extensive (Carl 1979). More complex burrow systems are associated with permanent colonies, while less favourable habitat is associated with transient occupancy and less extensive burrowing (Carl 1979). Analogous trends are seen at larger spatial scales where source-sink theory (Pulliam 1988) has been used to describe variation in populations across habitats. Much of arctic ground squirrel phenology is entrained by a long hibernation period lasting from seven to nine months (Buck and Barnes 1999a).

Review methods

A review of arctic ground squirrel publications was conducted using Web of Science and Google Scholar search engines. Post-1990 publication frequencies between arctic ground squirrels and other members of the genus *Urocitellus* were compared using Web of Science topic searches (accessed 24th March 2012) for exact phrases containing the common or scientific names of these species, including previous common and scientific names (in the case of arctic ground squirrels, *Urocitellus parryii*, *Spermophilus parryii*, *S. undulatus, Citellus parryii, C. undulatus, C. buxtoni, C. eversmanni, C. stejnegeri*, arctic ground squirrel). This can be assumed to provide a reasonably equitable index of the relative number of published papers for these species. Area of distribution for each species was retrieved from the IUCN red list database (IUCN 2010). For comparative purposes, similar search criteria were applied to other arctic herbivores. For two species of *Lemmus* (*trimucronatus* and *sibiricus*) formerly considered conspecifics, publication counts were grouped since these species perform very similar ecological roles and publications prior to recognition of the two species could not be specifically attributed.

Results and discussion

What is the role of arctic ground squirrels in northern ecosystems?

‘Keystone species’ and ‘ecosystem engineer’ define the roles of species in structuring communities. Ecosystem engineers create or maintain habitats and alter resource availability for other species, in terms of quantity, quality or distribution, causing state changes in the abiotic or biotic environment (Jones et al. 1994). Keystone species have a disproportionate effect on a community relative to their abundance or biomass (Power et al. 1996) and are crucial to community organisation and diversity (Mills et al. 1993). While keystone refers to a species' large impact, ecosystem engineer is a more process-oriented term (Wright and Jones 2006). Notably, keystones exclude species which modulate community organisation and diversity purely by virtue of their sheer pervasiveness.

Arctic ground squirrel burrowing activity generates clear geomorphic effects on their habitat. Burrows affect slope development by creating instability, and alter the drainage of soils, which can in turn affect soil chemistry (Hall and Lamont 2003). Arctic ground squirrels can cause persistent and extreme disturbance, contributing to spatial heterogeneity. In one area, they were estimated to excavate 2.5 tonnes of soil $ha^{-1}yr^{-1}$ (Price 1971). Fossil remains of arctic ground squirrel middens from 80 000 yr BP (Zazula et al. 2011) suggest that components of burrow systems can persist over long durations, even in the absence of new activity.

The edaphic changes created by arctic ground squirrels influence flora and other fauna, and affect vegetation by altering, and often greatly intensifying, the disturbance regime. Burrowing may promote growth of more disturbance-tolerant vegetation, as has been suggested for other burrowing species (e.g. Galvez-Bravo et al. 2011). Disturbance and therefore arctic ground squirrel activity, may facilitate canopy-forming shrubs (Myers-Smith et al. 2011). Soil ejected from burrows can also affect vegetation more locally, via burying. Burrows may be utilised by other burrowing species, which either take over these burrows or use vacant burrow systems. In some areas, hoary marmots *(Marmota caligata)* coexist with squirrels in burrows and also inhabit inactive squirrel burrow systems, while evidence of microtine use is also common in squirrel burrows (pers. obs.). Burrows can attract larger mammals such as grizzly bears and foxes which increase disturbance effects by digging up burrows when foraging for arctic ground squirrels.

Plants can be influenced by local fertilisation of soils with faeces around burrows. McKendrick et al. (1980) found available nitrogen, phosphorus and total ions to be elevated at the centre of burrow systems. This was associated with increases in vascular plants around burrows, particularly increases in grasses and decreases in *Dryas* and dwarf willow shrubs. Long-term exclusion of arctic ground squirrels leads to increased lichen (Gough et al. 2008). As yet it is unclear whether these vegetation transitions are a result of fertilisation, foraging, disturbance or more likely a combination of these pressures. The net result may be increased forage quality for both arctic ground squirrels and other herbivores.

Arctic ground squirrels are important nodes in terrestrial arctic food webs and are prey for both avian and terrestrial predators. Avian predators include golden eagles (*Aquila chrysaetos*, Bailey 1975), goshawks *(Accipiter gentilis)*, great horned owls (*Bubo virginianus*, Gillis et al. 2005) and gyrfalcons (*Falco rusticolus,* Poole and Boag 1988). Terrestrial predators include grizzly bears (*Ursus arctos horribilis)*, red foxes *(Vulpes, vulpes)*, coyote (*Canis latrans)* and lynx (*Lynx canadensis,* Gillis et al. 2005). Predators may depend increasingly upon arctic ground squirrels during low abundance of cyclic primary prey (Reid et al. 1997; Prugh 2005). Modified arctic ground squirrel density and distribution could therefore cause critical changes to the predation regimes occurring in northern ecosystems.

Arctic ground squirrels are also predatory. In the boreal forest, juvenile snowshoe hares *(Lepus americanus)* experienced 70% mortality within the first five days of life, of which arctic ground squirrels are responsible for at least 9% (O'Donoghue 1994). In a radio tracking study in coastal tundra, at least 4.5% of collared lemming (*Dicrostonyx groenlandicus)* individuals being monitored were killed by arctic ground squirrels (Boonstra et al. 1990).

The biological effects caused by burrowing activity are clearly sufficient to render arctic ground squirrels ecosystem engineers; however whether they are a keystone species is questionable. Arctic ground squirrels have strong effects on ecosystems by virtue of the combination of the *per capita* effects they exert and the high abundances they reach. They can contribute to a high proportion of storage and flow of energy within their habitat. In the boreal forest of the Kluane region, southwest Yukon, where density is relatively low (Gillis et al. 2005), arctic ground squirrels comprised approximately 17% of vertebrate herbivore biomass, and account for 22% of energy flow in the system (Krebs 2001). In alpine and arctic tundra habitats, their densities, and hence associated biomass and energy flow appear to be much higher (e.g. >50% in alpine tundra, Hik et al. unpublished data).

Density is a major factor contributing to arctic ground squirrel's high ecological importance. In more southerly latitudes, where congeneric species overlap more with human activity, the combination of ecosystem engineering and high density most commonly results in the definition of these ground squirrel species as pests (e.g. Ling et al. 2009), however, there is no term for the overall effect of these species on communities that does not imply a negative role. This highlights the lack of acknowledgement of the importance of such species. In Pleistocene environments, where densities are thought to have been higher, this engineering role may have been even greater. I conclude that these species should be considered ecosystem engineers in tundra ecosystems but are probably not ecosystem engineers given their high densities are a key factor determining their impacts.

What determines the distribution and density of arctic ground squirrels?

Arctic ground squirrels have a wide geographic distribution (Fig. 2.1a) and occupy a broad niche. From current and paleoecological distributions a number of factors determining distribution and density can be inferred. Much of the historical distribution of arctic ground squirrels, spanning >740 000 years has been associated with mammoth steppe-tundra (Gaglioti et al. 2011; Zanina et al. 2011; Zazula et al. 2011). This habitat was highly fertile and dominated by graminoids and forbs. It was characterised by a cold and arid climate, low precipitation, and greater active layer thaw than in current arctic tundra, facilitated by shallower snow pack (Gaglioti et al. 2011; Walker et al. 2001). This would have allowed a sufficient depth of unfrozen soil for burrow establishment. Arctic ground squirrels have persisted through considerable variation in climate, including several glacial cycles (Eddingsaas et al. 2004); the current Holarctic distribution with warmer wetter conditions than glacial intervals of the late Pleistocene probably represents a considerably more restricted distribution than during much of this species' history (Zazula et al. 2011).

Currently, arctic ground squirrels are found from northeast Russia across northwest Canada (Banfield 1974; Hall 1981). Arctic ground squirrels habitats include continuous (Mayer 1953) and discontinuous arctic tundra (Boonstra et al. 1990), alpine tundra (Doak and Loso 2003; Gillis et al. 2005), areas of meadow within boreal aspen and spruce stands (de Vos and Eay 1959; McLean and Towns 1981; McLean 1985; Byrom and Krebs 1999; Hik et al. 2001) and boreal forest (Byrom and Krebs 1999; Karels and Boonstra 2000; Karels et al. 2000; Frid and Turkington 2001). Across these habitats, considerable variation in density and demography has been observed (Table 2.1).

Boreal forest is generally considered marginal habitat. In the southwest Yukon, boreal forest supported lower population densities than alpine tundra, and also had greater fluctuations in density (Gillis et al. 2005). Boreal populations have occasionally become locally extinct and may represent examples of population sinks (Donker and Krebs 2011). The marginal nature of boreal forest is also supported by evidence from fossil middens. Zazula et al. (2007, 2011) found fossil middens of arctic ground squirrels in Quartz Creek, Yukon Territory, dating back to ~25kya and ~80kya. Presently, arctic ground squirrels are rare in this area. These areas are currently covered by black spruce (*Picea mariana*) forests, with shallow soil active layers and poor drainage, which provide a suboptimal environment for the establishment of arctic ground squirrel colonies. Open tundra habitats represent more suitable habitat and maintain more viable and dense populations.

Factors affecting density differ considerably between habitats. In arctic tundra, density may be limited by abiotic factors in particular, the suitability of microhabitats. Permafrost accompanied by a thin active layer can limit the ability of squirrels to dig burrows, while poor drainage of soils can limit the suitability of burrows (Quay 1951; Mayer 1953; Carl 1971; Batzli and Sobaski 1980; McLean 1985; Poole and Boag 1988). For this reason, at the more northern extent of the range and at high altitudes, squirrels were limited to microhabitats where the seasonal depth of thaw is sufficient and areas with good drainage, such as raised areas (Quay 1951; Mayer 1953) and south facing slopes (Mayer 1953; Price 1971). In the boreal forest, density may be affected more by biotic processes such as predation. Predation and food can both limit abundance in the boreal forest (Byrom et al. 2000). Predation may have particularly high impact in boreal forest because predator detection is impeded by dense vegetation and group vigilance, and alarm-calling strategies, commonly employed in tundra, may be less effective. Within the boreal forest, areas with greater visibility were more likely to retain active burrow systems (Karels and Boonstra 1999). Low elevation meadows tended to support greater population densities than those within forest stands (Donker and Krebs 2011). This may be, in part, because of greater visibility afforded by meadow areas.

Detailed records of arctic ground squirrel occurrence are relatively rare. Consequently, much of our understanding of the population dynamics of arctic ground squirrels derives from a boreal forest region at the southern limit of their range in the southwest Yukon. This represents marginal habitat, where dynamics differ substantially from, and are likely to be unrepresentative of core populations. There are relatively few long-term census records or spatial replicates of density estimates for any habitat type. In addition, different methodologies of density estimation provide different biases, so that estimates are not directly comparable. As a result, it is difficult to generalize the relationships between habitat type and density or population processes. To make better use of this species as an indicator of holarctic change and understand how it is responding to change, we need to understand the processes occurring in both core populations and marginal populations.

How might climate change affect arctic ground squirrels?

Past climatic variation appears to have affected arctic ground squirrel distribution (Zazula et al. 2011) and further responses should be expected in the future. Arctic ground squirrels face a wide range of biotic and abiotic stressors that may become altered in frequency and intensity as climate changes (Table 2.2). These have the potential to cause a wide range of responses. The magnitude and direction of responses will be dependent on the extent of warming and changes in many other environmental conditions (Table 2.2). I discuss some of the pressures arctic ground squirrels may face as the Arctic transforms under climate change below. Among the most consequential are warming temperatures (Fig. 2.1b), hydrological changes, cryospheric changes (Fig. 2.1c and d), and habitat alterations.

Warming temperatures

Arctic ground squirrels are adapted for cold climates; their thick fur and short limbs, which aid heat retention, may be maladaptive as the climate warms. Certain basic mechanisms of heat loss, such as sweating, are also lacking (Chappell 1981). Exposure to temperatures above 30°C for 55 minutes is lethal (Sullivan and Mulen 1954).

Rising temperatures could increase the costs of summer thermoregulation for arctic ground squirrels. Land surface temperatures in the Arctic are projected to rise by 3-5°C in summer between 1990 and 2090 (ACIA 2005). Behavioural thermoregulation is a significant component of thermoregulation for arctic ground squirrels, which use burrows to avoid rain, cold and heat (Watton and Keenleys 1974; Long et al. 2005).

Increased burrow use for thermoregulation could reduce foraging time and may reduce seasonal mass gain. Arctic ground squirrels gain considerable mass throughout the active season (Buck and Barnes, 1999b) and high mass increases survival (Murie and Boag 1984; Rieger 1996), reproductive success (King et al. 1991; Neuhaus 2000) and offspring quality (Trombulak 1991) in many ground squirrel species. Reduction in the amount of time spent foraging because of shade-seeking behaviour could reduce population viability.

Although arctic ground squirrels are a well-studied model organism for hibernation energetics (e.g. Erikson 1956, Barnes 1989; Pastukhov et al. 1995; Barnes and Buck 2000, Buck and Barnes 2000), data is insufficient to predict how warming will affect overwinter survival and condition. Winter temperatures are projected to increase by an average of 4 to 7°C between 1990 and 2090 (ACIA 2005, Fig 2.1b). While extensive data exists concerning the effect of local temperature upon hibernation in laboratories (Table 2.2), the main limits to our knowledge of hibernation ecology concern the effect of warmer climate on the temperature experienced by an individual within a burrow. Air temperature may correlate poorly with burrow temperatures. Snow cover, vegetative cover, topography and the extent of nesting material insulating burrows can all affect both minimum and mean burrow temperature (Buck and Barnes 1999a) and microhabitat selection of burrow sites reflects the advantage to be gained from a well-insulated burrow during the winter (Carl 1971; Buck and Barnes 1999a). Under climate change, burrow temperatures could either increase (e.g. because of higher temperatures, greater vegetative cover and more snow insulation) or decrease (e.g. if thawing events leave burrows exposed to cold winter temperatures). Further understanding of how habitat and climate affect burrow temperature is needed to discern whether changes in hibernation duration could alter energy balances and consequently the cost of hibernation.

Hydrological changes

Flooding is a major cause of mortality in arctic ground squirrels. Increased rainfall, more intense rainfall, or rapid periods of snowmelt can all cause flooding. Precipitation increased by 4% in areas north of 50°N between 1945 and 1995 (IPCC 2007), and is expected to increase by 7.5 to 8.1% by 2070 to 2090 (ACIA 2005), reflecting some of the greatest increases globally. Increased winter precipitation, causing increased snow pack combined with elevated spring temperatures may also cause intense periods of spring flooding. Flooding of burrows can cause population decline through direct mortality (e. g. Robson 1993; Bowen and Read 1998) or by displacing individuals and appears common for arctic ground squirrel colonies in more marginal habitat (Carl 1979). Although in other species, displaced animals can return to flooded burrows (Giger 1973), individuals would still be likely to incur significant costs. The timing of flooding may be critical; if flooding occurs between parturition and weaning, or during hibernation, the chances of mortality are increased (Robson 1993).

In addition to flooding events, permanent waterlogging of soils may increase as permafrost thaws. This could greatly reduce habitat suitability for squirrel colonies, although establishment of vegetation with more extensive root systems, such as canopy forming shrubs, could improve local drainage of soils (Fig. 2.2).

Cryospheric changes

Northward range expansion and increase in density of arctic ground squirrels may be facilitated by permafrost thaw in well drained areas. For colonies to establish, the active layer of unfrozen soil must be sufficiently deep that burrow systems can be excavated or sufficient drainage must occur to create a drier upper layer of soil where burrowing can occur (Quay 1951; Batzli and Sobaski 1980). Permafrost is expected to thaw to create deeper active layers and limits of permafrost extent are also expected to shift northward (Lawrence and Slater 2005; IPCC 2007, Fig. 2.1c and d). A reduction in permafrost and increase in active layer depth could increase the proportion of microhabitats that have sufficient active layer depth for burrowing and facilitate increases in the density and extent of arctic ground squirrels towards the northern and altitudinal extremes of their distribution.

Substantial complexity surrounds the relationship between permafrost thaw and its effect on arctic ground squirrels; trends are likely to vary regionally depending on the interactions between, thaw, moisture levels, drainage and vegetation change (Fig. 2.2). Increases in soil moisture are associated with permafrost thaw (Smith 2010). Waterlogging of soils may limit the extent to which increased active layer depth increases habitat suitability. However, as thaw continues and in areas of discontinuous permafrost, where permafrost is breached, drainage may be facilitated and drying could occur (Smith et al. 2005). Perhaps somewhat counter-intuitively, warming could also result in vegetation changes that alter seasonal thaw of soils. If canopy forming species such as boreal forest trees and shrubs increase in density, they shade soils in summer, reducing thaw (Bockheim et al. 1998; Walker et al. 2001; Blok et al. 2010). However, shrubs with low-lying canopies trap snow in winter, providing insulation and elevating soil temperature and may counter this effect (Sturm et al. 2001). The impacts of permafrost thaw on arctic ground squirrels are therefore likely to vary substantially, depending on a wide range of local contingencies, which determine whether active layer depth is sufficient for burrowing and if areas are dry enough for habitation.

Phenology

Changes in matching between life history events and seasonal phenologies of weather and vegetation may affect fitness of arctic ground squirrels. Snow cover is a major determinant of biotic phenology in the Arctic. Changes in timing of snowmelt, timing of snow onset and duration of snow cover have numerous effects on mammal population dynamics (Forchhammer et al. 2008). Increased forage availability early in the season can increase reproductive success (Kreuzer and Huntly 2003) and improve survival (Morrison and Hik 2007). Advances in snowmelt are strongly associated with warming, have been observed across 80% of the Arctic and are projected to continue, but are characterised by high regional variation (Callaghan et al. 2011; Liston and Hiemstra 2011, Fig. 2.3). Increased winter precipitation can increase snow pack and could delay snowmelt and forage availability in some areas, depending on the extent of acceleration in snowmelt.

The effects of changes in snowmelt timing will depend on how life history events shift to match changing phenology. Squirrels experience significant periods between arousal and emergence where they remain in burrows (Buck and Barnes 1999b), which may allow plasticity in emergence dates without requiring altered hibernation timings. However, cues for many of these events are unknown. Spatial variation in phenology reflects variation in climate in arctic ground squirrels, but although associations exist between climate and phenology, events do not fully match seasonal climatic events (Sheriff et al. 2011). Premature emergence can cause substantial mortality as a result of severe weather (Morton and Sherman 1978). Relatively conserved emergence dates in arctic ground squirrels could be driven by strong selection against emerging too early (Buck and Barnes 1999b). If arctic ground squirrels are unable to respond to shifting phenologies, negative population consequences are likely.

Habitat change

Habitat transformations could extirpate or reduce populations in more southerly and climatically milder areas. Encroachment of woody shrub and boreal forest species to higher latitudes and elevations, and increases in density in their current range, are occurring (Sturm et al. 2001; Tape et al. 2006; Danby and Hik 2007a, b; Myers-Smith et al. 2011). Encroachment of woody species into areas of more low-lying vegetation may have adverse effects on populations across many latitudes (Fig. 2.4).

Boreal forest provides poor arctic ground squirrel habitat (Eddingsaas et al. 2004; Gillis et al. 2005; Donker and Krebs 2011). Differences in the density and dynamics of squirrel populations between boreal forest and alpine tundra habitats have been attributed to differing predator species and variation in the ability of squirrels to detect predators between visually obstructed and open habitats. Even during low predator densities in the boreal forest, squirrels experienced symptoms of chronic stress, unlike in alpine tundra (Hik et al. 2001). Chronic stress levels were attributed to the inability of squirrels to detect predators at distance, caused by taller vegetation associated within the boreal habitat. Energetic costs associated with increased investment in predator sensitive behaviours in more visually obstructed habitats may further reduce viabilities of squirrel populations in the boreal forest.

Less is known about how arctic ground squirrels are affected by shrub encroachment. Reduced detectability of predators could increase predation mortality directly, but is often observed to have indirect effects by increasing predator-sensitive behaviour (e.g. Sharpe and Van Horne 1998; Mateo 2007) and reducing time available for foraging. In some contexts, taller vegetation may be beneficial, providing cover and reducing the efficacy of predator attack (Pietrek et al. 2009). Arctic ground squirrels evolved in tundra environments that included much shorter vegetation than those they inhabit today (Gaglioti et al. 2011). Where future vegetation change includes extensive increases in cover of shrub and tree species, densities of arctic ground squirrels will likely decline.

Arctic ground squirrels as drivers of ecosystem change

Altered arctic ground squirrel distribution and density associated with global warming and human activities have the potential to exacerbate and alter trajectories of ecosystem conversion. Arctic ground squirrels are likely to be affected by some of the key changes projected in the cryosphere, vegetation and climate (Table 2.2, Fig. 2.2). Opportunities for expansion in distribution and density may occur in some northern and colder areas of the Arctic, as permafrost melts and soil active layer depths increase, although increased moisture may make other areas less habitable. Populations may become diminished, transient or extirpated, as woody species encroach and increase in density on previously more open areas.

Where their densities increase, arctic ground squirrels may alter soil processes, increase disturbance and substantially modify plant communities and vertebrate food webs. Reduced densities of arctic ground squirrels, conversely, have the potential to remove a dominant ecosystem engineer and prey species. Ground squirrel predators may either be adversely affected by a loss in potential prey, or may affect other prey species as they focus more on alternative prey. Arctic ground squirrels will be influenced by the future climate and vegetation changes, and any changes in their densities and distributions will alter the ecosystem through a variety of feedback processes. Consequently, this species should feature prominently in tundra-climate change research efforts.

How well is the ecology of arctic ground squirrels represented in scientific literature?

Despite their broad range and considerable functional role, little is known about arctic ground squirrel distribution. In North America, most ecological studies of arctic ground squirrels have been conducted in Alaska and the southwest Yukon (Fig. 2.1a) and very little scientific information is available from the interior Canadian arctic distribution. Despite arctic ground squirrels being distributed across an area an order of magnitude greater than all other species of *Urocitellus*, fewer publications exist than for some more southerly species. Amongst southern species, an approximately linear relationship exists between geographic distribution and number of ecological publications, however, the number of arctic ground squirrel publications falls distinctly below this relationship (Fig. 2.5). When compared to other northern herbivores such as the tundra vole (*Microtus oeconomus*, 123 publications), northern collared lemming (*Dicrostonyx groenlandicus*, 37 publications) and snowshoe hare (*Lepus americanus*, 359 publications), the arctic ground squirrel had few publications (34 publications). Species with fewer publications than arctic ground squirrels generally had restricted ranges (arctic hare, *Lepus arcticus*, 11 publications), or were small and less conspicuous (*Lemmus spp.*, 14 publications, northern red-backed vole, *Myodes rutilus*, 21 publications).

How could better and more instructive representation be achieved?

Much can be gained from studies of the density, distribution and ecology of arctic ground squirrels in wider range of contexts. The need for baseline data to detect environmental change is well documented (Pauly 1995; Papworth et al. 2009) and there is some urgency to sustain these efforts in the Arctic (Hik and Boonstra 2004). At the most basic level, recording of presence and absence, population density and burrow density of arctic ground squirrels would provide a baseline from which changes throughout their range could be monitored. Currently much of this information is derived from studies in boreal forest and may not easily be extrapolated to tundra habitats. This information could be relatively easily collected and would contribute greatly to our understanding of ecosystem processes in the northern ecosystems.

The three major priorities for future research include:

1. Identification of habitat and climatic effects on density across the current arctic ground squirrel distribution.
2. Determining the effect of permafrost thaw on burrowing behaviour and overwinter survival.
3. Assessing the effect of local density of arctic ground squirrels on ecosystem processes.

Conclusion

Arctic ground squirrels are underrepresented in the ecological literature. They are ecosystem engineers that exert a high impact on their habitat and have the potential to be drivers of future ecosystem change. They are widespread and hence could be used to monitor changes over large spatial extents. Priorities for research should include more comprehensive information about their current distribution and abundances across the species range, climatic and environmental factors driving population dynamics in core habitat areas, comparison of lab-based and in-situ thermal physiology, and responses to different habitat types at both behavioural and population levels.

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Table 2.1. Summary of population densities of arctic ground squirrels in different habitats. Mean density across years are reported based on values reported by authors. Variation in estimation technique is highlighted as well as variation in local habitat quality.

		Mean density per hectare									
Habitat	May	Jun	July	Aug	Sept	Other	Years	Location	Geographic area	Estimation technique	Reference
Low Arctic tundra		0.4	1.7	0.7			1976-1977	71°29N 157°25W	northern Alaska, USA	MNA/total area suitable for burrowing	Batzli & Sobaski 1980
Low Arctic tundra		0.2	0.6	0.4			1976-1977	71°29N 157°25W	northern Alaska, USA	MNA/total area suitable for burrowing	Batzli & Sobaski 1980
Low Arctic tundra	2.6	1.6	6.9	4.8	3.7		1960	68°3'24''N 165°46'33'' to 53"	northwest Alaska, USA	MNA/area	Carl 1971
Low Arctic tundra		0.01 - 0.04					1991-1992	69°48'N, 122°40'W	northern NWT, Canada	Tracking plates to estimate burrow activity, estimated density within range given	Reid et al. 1995
Boreal Forest	1.7		2.2				1996-1998	61°N 138°30W	southwest Yukon, Canada	Capture recapture estimates/area	Karels et al. 2000
Boreal Forest			0.4				1998-2003	61°N 138°30W	southwest Yukon, Canada	Capture recapture estimates/area	Gillis et al 2005
Alpine			1.6				1998-2003	61°N 138°30W	southwest Yukon, Canada	Capture recapture estimates/area	Gillis et al 2005
Alpine				5.5			2008-2009	61°1’6’’N 138°37’ 34”W	southwest Yukon, Canada	Spatially explicit capture recapture estimates	Donker and Krebs, 2011
Low elevation meadow						13-16	1988-1990	60°47’N 137°40’W	southwest Yukon, Canada	Live trapping (MNA), undefined timeframe	Lacey et al, 1997
Low elevation meadow				1.5			2008-2009	60°59’56’’N 138°33’31’’W	southwest Yukon, Canada	Spatially explicit capture recapture estimates	Donker and Krebs, 2011

Table 2.2. Summary of potential climate change induced stressors affecting arctic ground squirrels. Possible effects and interactions with density are suggested (potential effect column refers to likely influence on density). Possible consequences for arctic ground squirrel populations are given, as well as limits within which these might be expected to be observed. Key areas where information is missing for effects of each stressor are also described. References in bold refer directly to arctic ground squirrels, references in normal typeface draw information from other species, those in italics refer to changes in the environment.

Stressor	Potential effects	Effect	Consequences	Missing information	Conditions/Limits	Related References
Warming temperatures	Reduced cost of torpor	+	Better condition upon emergence	Relationship between above ground temperature and temperature in nests within burrows	Up to burrow temperatures 0-16°C	**Barnes & Buck 2000**
	Increased fat catabolism	+	Greater lean mass upon emergence	Effect of temperatures outside natural variability upon changes in lean mass during hibernation	Up to burrow temperature of 4-8°C	**Buck & Barnes 2000** **Galster & Morrison 1975** **Shao et al. 2010**
	Increased torpor bout length requiring fewer cycles of arousal	+	Better condition upon emergence	Relationship between above ground temperature and temperature in nests within burrows	Up to burrow temperature 0°C	**Buck & Barnes 2000** Geiser & Kenagy 1988
	Reduced torpor bout length requiring more cycles of arousal	-	Poorer condition upon emergence	Relationship between above ground temperature and temperature in nests within burrows	Burrow temperatures above 0°C	**Buck & Barnes 2000** Geiser & Kenagy 1988
Increased max. temperatures	Heat stress	-	Mortality	Effect of other temperatures and durations of exposure on mortality.	Above 30°C	**Sullivan & Mulen 1954**
	Increase temporal foraging opportunities	+	Improved condition	Effect of climate change on standard operative temperature	Up to standard operative temperatures 17°C	**Long et al. 2005** **Watton & Keenleys 1974**

Stressor	Potential effects	Effect	Consequences	Missing information	Conditions/Limits	Related References
	Increased burrow use Reduced/more synchronised foraging	-	Poorer condition	Effects of warm periods upon synchrony of foraging activity Effect of climate change on standard operative temperature	Above standard operative temperatures of 33°C	**Long et al. 2005** **Watton & Keenleys 1974**
Increased spring and summer precipitation	Increased burrow use Reduced/more synchronised foraging	-	Poorer condition	Effects of rain periods upon synchrony of foraging activity		**Long et al. 2005**
	Burrow flooding	-	Mortality or energetic costs	Direct measurement of extent of effects of burrow flooding	Unknown	Bowen & Read 1998, Robson 1993
Increased winter precipitation	Burrow flooding	-	Mortality or energetic costs	Direct measurement of extent of effects of burrow flooding	Unknown	Bowen & Read 1998, Robson 1993
Increased spatial extent of precipitation	Increased synchrony across populations	-	Reduced persistence	Concurrent population dynamic data of populations spanning different spatial scales	Unknown	**Liebhold et al. 2004**
Advanced snowmelt	Increased forage availability during breeding and in spring	+	Increased survival (especially for males) and reproductive success	Potential for plasticity/adaptation in emergence timing. Estimates of and drivers of spring male mortality	Unknown	Kreuzer & Huntly 2003 Morrison & Hik 2007
	Burrow flooding	-	Mortality, increased energetic costs	Potential for plasticity/adaptation in emergence timing. Estimates of and drivers of spring mortality	Unknown	Bowen & Read 1998, Robson 1993
	Blocking of burrows with ice	-	Mortality, increased energetic costs	Potential for plasticity/adaptation in emergence timing. Estimates of and drivers of spring mortality	Unknown	**Carl 1971**

Stressor	Potential effects	Effect	Consequences	Missing information	Conditions/Limits	Related References
	Advanced emergence	-	Increased reproductive output	Potential for plasticity/adaptation in emergence timing.	Unknown	Vanvuren & Armitage 1991
	Mismatch between plant productivity and life history events	-	Increased juvenile mortality, lower condition	Potential for plasticity/adaptation in emergence timing. Estimates of and drivers of spring mortality	Unknown	Hoye & Forchhammer 2008
Increasing winter snow depth	Increased insulation of burrows, lower hibernation costs	+	Better condition upon emergence	Relationship between snow cover and within-nest burrow microclimate	Unknown	
Reductions in winter snow cover and depth	Reduced insulation of burrows, higher hibernation costs	-	Poorer condition upon emergence	Relationship between snow cover and within-nest burrow microclimate	Unknown	*Prowse, Furgal, Melling et al. 2009b*
Freeze thaw cycles	Alter forage biomass/ composition in spring	?	Unknown	Quantification of effect of freeze thaw cycles on forage	Unknown	*Grogan. 2004* *Kreyling, 2010*
	Less cover from predation in early season	-	Predation mortality, poorer condition	Measurement of effect of snow cover after emergence on predation mortality	Unknown	Callaghan et al. 2004
Permafrost thaw	Increased active layer depth opening more sites for burrowing	+	Increased population density	Comparative evidence of relationship between thaw depth and colonisation	Unknown	**Batzli & Sobaski 1980**
Cryoturbation	Burrow system collapse	-	Colony loss	Direct evidence	Unknown	

Stressor	Potential effects	Effect	Consequences	Missing information	Conditions/Limits	Related References
Increased soil moisture	Decreased area suitable for burrowing	-	Reduced population density	Quantitative experimental evidence of the effect of soil moisture on colonisation	Unknown	**Barker & Derocher, 2010** **Quay 1951; Mayer 1953; Carl 1971;** **Batzli & Sobaski 1980;** **Poole & Boag 1988**
Drying of soils	Increased area suitable for burrowing	+	Increased population density	Quantitative experimental evidence of the effect of soil moisture on colonisation	Unknown	**Quay 1951; Mayer 1953; Carl 1971;** **Batzli & Sobaski 1980;** **Poole & Boag 1988**
Encroachment of boreal species	Reductions in visibility of the environment	-	Higher predation mortality, higher energetic costs	Relationship between visibility and mortality, foraging behaviour and condition	Rate of boreal encroachment	**Barker & Derocher, 2010** **Hik et al. 2001** **Gillis et al. 2005** **Karels & Boonstra 1999**
	Increased insulation of ground, lower seasonal thaw	-	Reduced colonisation potential	Comparative quantitative evidence of relationship between thaw depth and colonisation	Unknown	Anisimov & Reneva 2006; Cannone & Gughelmin 2009
Encroachment of shrubby species	Reductions in visibility of the environment	-	Higher predation mortality, higher energetic costs	Relative costs and benefits of shrub cover	Rate of shrub encroachment	
		-	Greater infanticide	Further quantification of infanticide incidence and conditions	Rate of shrub encroachment	**McLean 1983, Steiner 1972**
	Increase in cover from predators	+	Lower predation mortality, lower predation cost	Relative importance of shrub as protective cover vs visual obstruction	Rate of shrub encroachment	
Increase in vegetation height and density	Reduced perpetuation of calls	-	Higher predation mortality, greater vigilance costs Allee effects	Effect of habitat on call transmission. Potential for adaptation of calls to habitat. Presence or absence of allee effects.	Rate of boreal and shrub encroachment	**Perla & Slobodchikoff 2002**

Stressor	Potential effects	Effect	Consequences	Missing information	Conditions/Limits	Related References
	Increased biomass and forage availability	+	Increased density	Direct evidence	Unknown	**Byrom *et al.* 2000**
Changing vegetation	Declines in seed forage	-	Increased mortality especially breeding males	Ability to adapt and gain sufficient nutrition from alternate food sources	Rate of graminoid biomass reduction	**Wilber & Musacchia, 1950** **Frank *et al.* 2008** **Shao et al. 2010**
	Declines in forb biomass	-	Poorer condition	Ability to adapt and gain sufficient nutrition from alternate food sources	Unknown	**Batzli & Sobaski 1983**
Longer growing seasons	Increase in duration of available forage	+	Better condition prior to hibernation	Plasticity and potential for adaptation in emergence and hibernation timing	Unknown	
New diseases and parasites	Increase in disease and parasite load	-	Increased mortality, poorer condition	Current diseases and parasites, susceptibility to likely emerging diseases	Unknown	*Kutz et al. 2009*

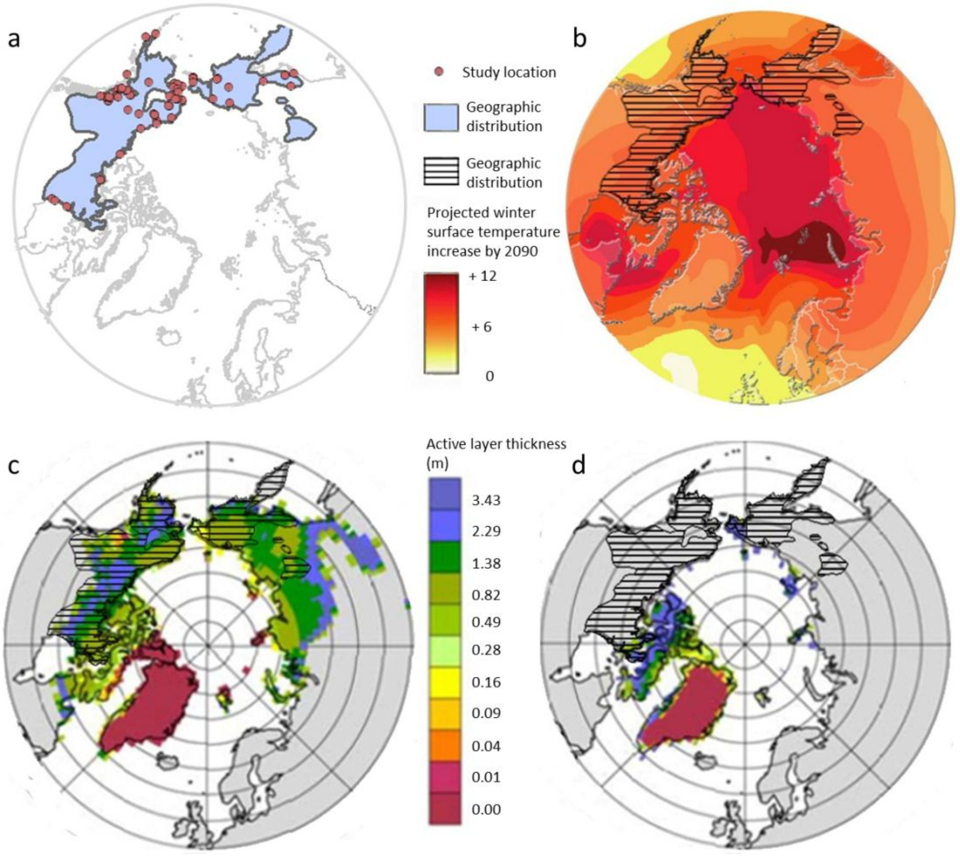

Figure 2.1. Distribution of arctic ground squirrels and overlap with areas of climatic and cryospheric changes. a) The current distribution of arctic ground squirrels and major study locations. Large areas of the distribution have received little attention particularly the interior Canadian Arctic. b) Projected increases in winter temperature in the Arctic and overlap with current squirrel distribution, adapted from ACIA (2005) and IUCN (2010). c) Current (end of 20th Century) and d) projected (end of 21st Century) permafrost extent shown by the ensemble coloured area, a dramatic reduction in extent overlapping with current squirrel distribution is projected, adapted from Lawrence and Slater (2005) and IUCN (2010).

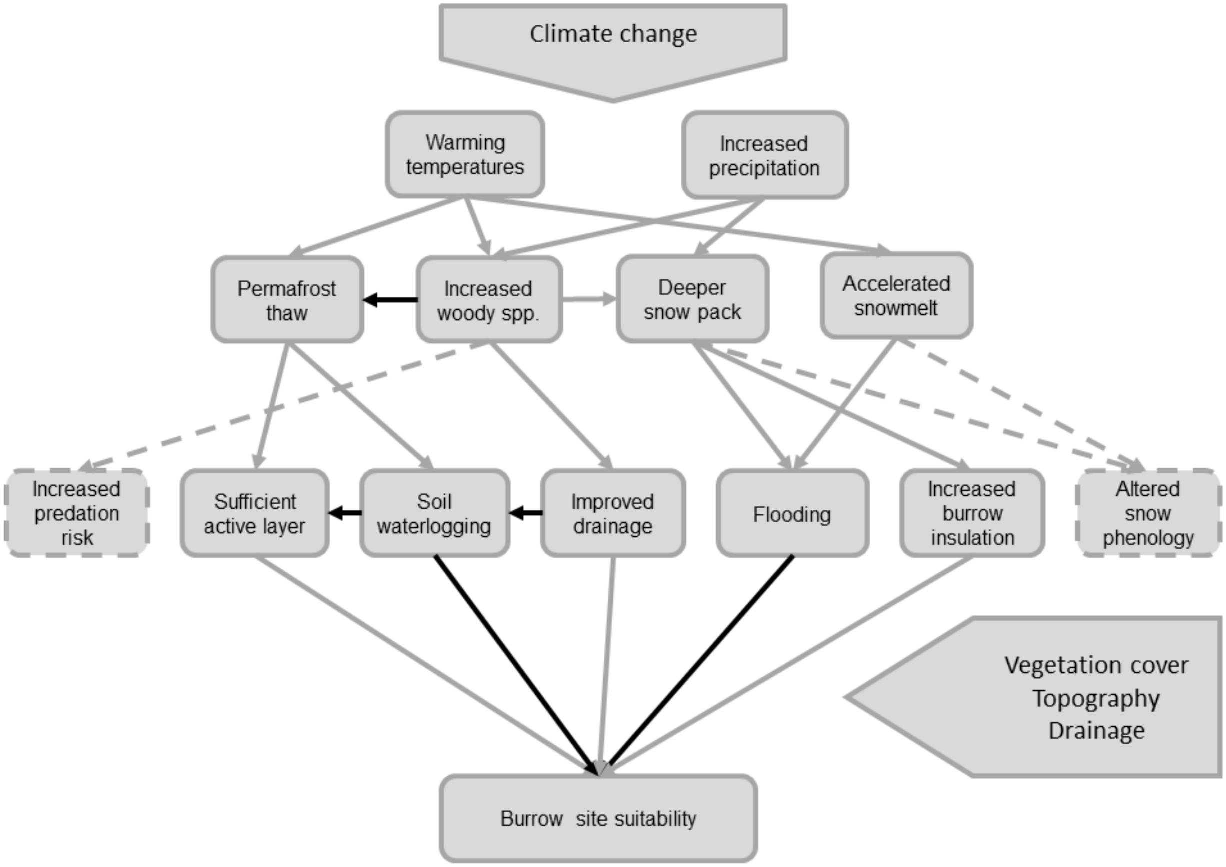

Figure 2.2. Diagram summarising some potential interactive effects of hydrological and cryospheric changes on arctic ground squirrel burrow site suitability. Broken arrows show additional indirect effects on squirrel fitness mediated through biotic interactions.

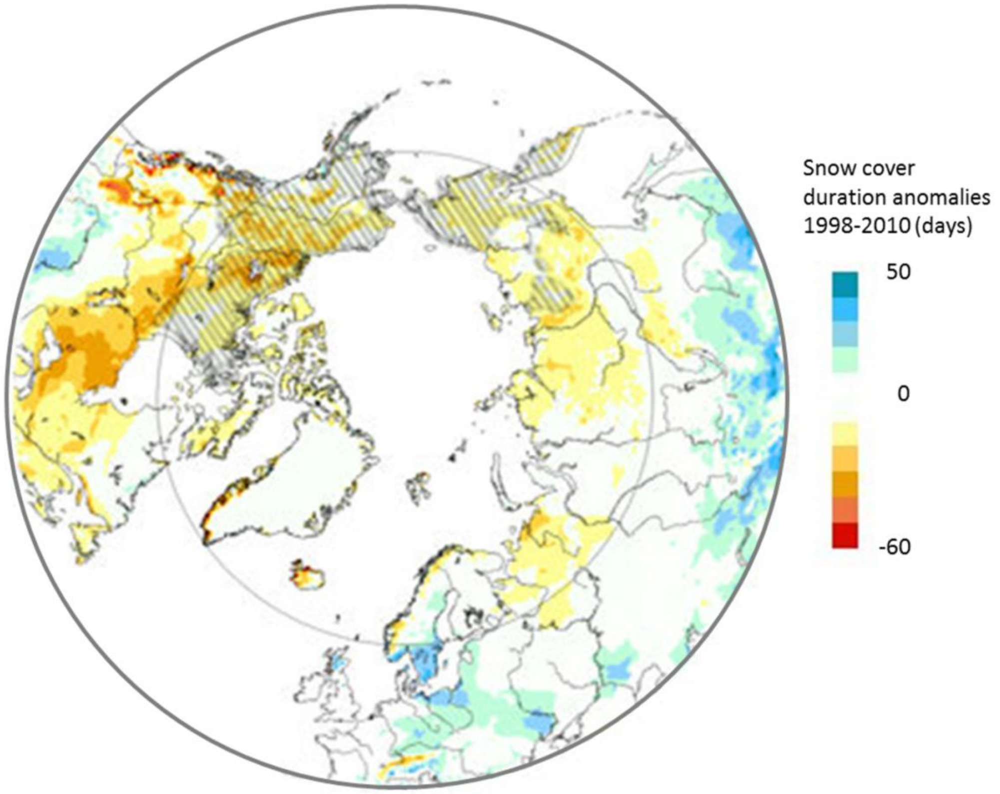

Figure 2.3. Changes in spring snow cover duration from 1998 to 2010 and overlap of high areas of decreased snow cover with current arctic ground squirrel distribution (hatched area), adapted from Derkson et al, (2010) and IUCN (2010).

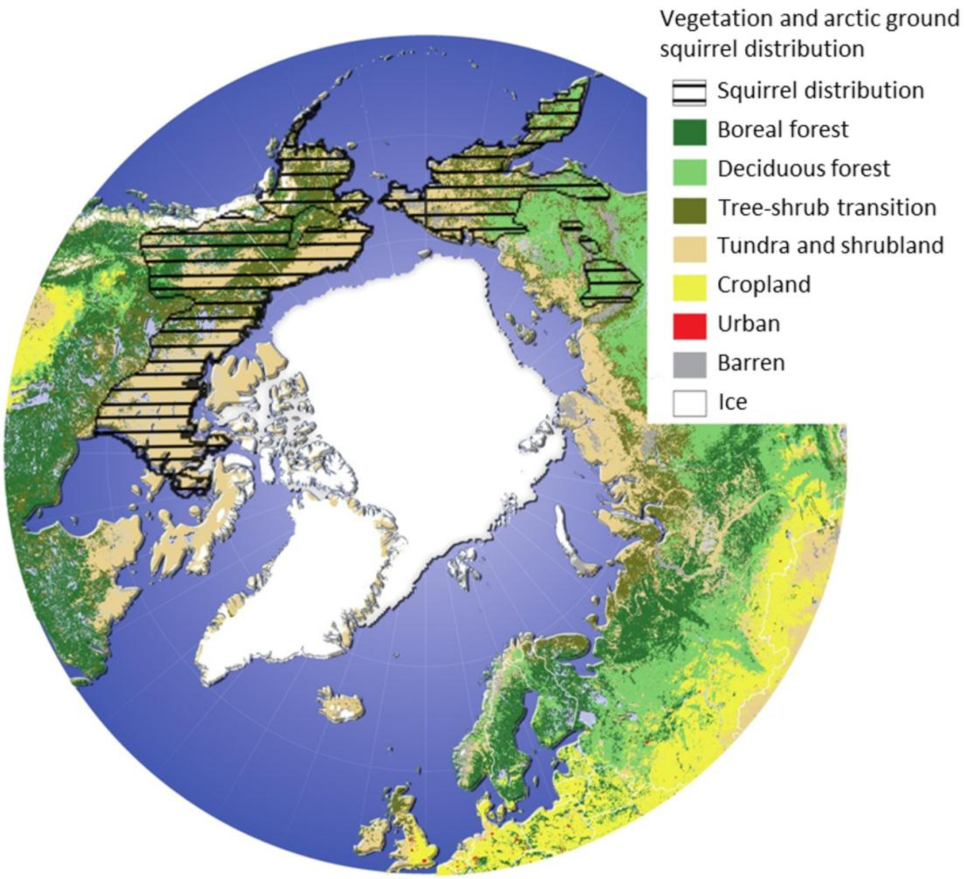

Figure 2.4. Current distribution of arctic ground squirrels across current vegetation types. The current distribution is bounded to the southern extent by coniferous and deciduous forest. Northward expansion of the forest would substantially alter much of arctic ground squirrel habitat presently occupied. Adapted from IUCN (2010) and UNEP/GRID-Arendal (2008).

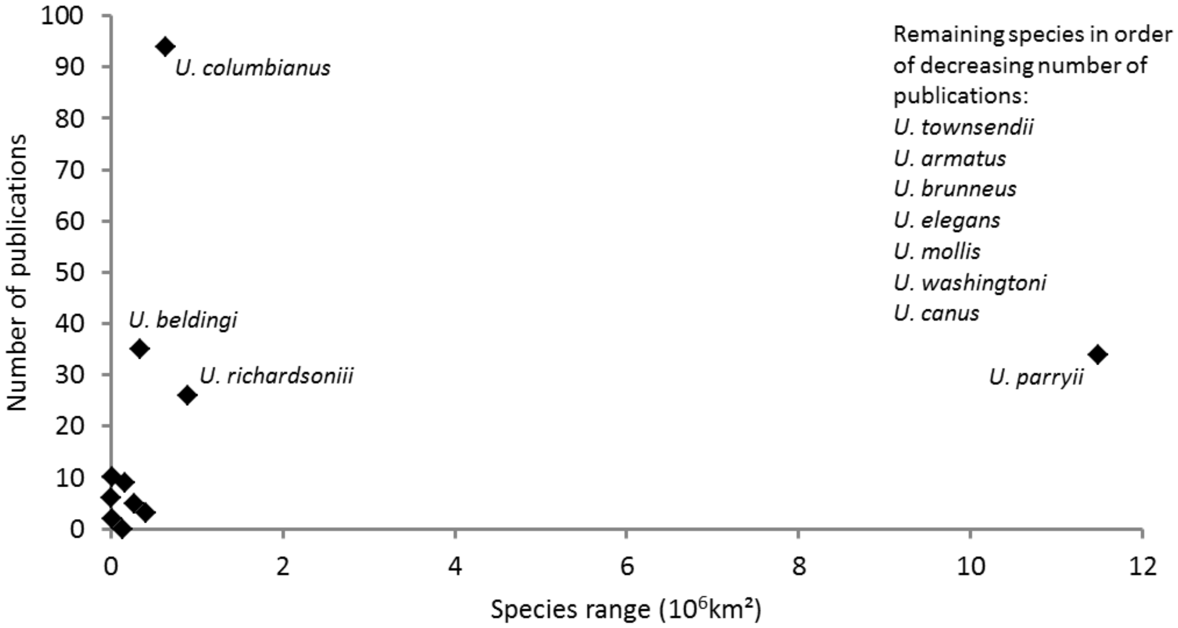

Figure 2.5. Number of ecological publications (from Web of Science, as of 24 March 2012) and geographic range for species of the genus *Urocitellus*. Species names are also shown. Arctic ground squirrels can be seen to receive a relatively low number of publications despite a much large species range than other ground squirrel species.

Chapter 3

Comparison of emigration and transience models for estimating survival and identifying temporary habitat associations for a central-place forager, the arctic ground squirrel (*Urocitellus parryii*)

Introduction

Survival estimates are used to assess population status, infer habitat suitability and evaluate management decisions (Anders and Marshall 2005; Calvert and Gauthier 2005; Johnson 2007; Alisaukas et al. 2011). However, survival estimates are sensitive to many population processes and behavioural responses to habitat suitability. Differences in survival estimates between habitats of differing suitability may reflect variation in the bias associated with violation of model assumptions caused by responses to habitat, rather than biological differences in survival. Techniques used to estimate survival must account for variation in behaviour that influences these estimates. In particular, temporary associations of individuals with different habitats may vary with habitat suitability and have the potential to cause systematic biases in survival estimates. Temporary associations may occur when individuals have a single interaction within a habitat, for example when travelling through an area during dispersal. Temporary associations may also be more habitual, including repeated movements and seasonal habitat preferences of individuals.

Survival models have been developed to incorporate temporary associations with habitat caused by occurrence of transient individuals and temporary emigration of residents. Transients are individuals that have a single short-term association with an area, and are distinct from the resident population. Transients may be common where dispersing individuals pass through habitats or where territoriality excludes a high proportion of new immigrants. Temporary associations with habitats also occur when individuals temporarily leave a focal habitat and may occur when preferred habitat varies temporally, either due to seasonal changes in habitat quantify or temporal changes in individual needs and behaviours. These individuals may be considered part of the resident population, but become temporarily absent. Models have been developed to incorporate temporary associations with habitat in to survival estimation. Transience models reduce negative bias in survival and positive bias in abundance caused by transient individuals (Pradel et al. 1997; Hines et al. 2003; Clavel et al. 2008), while robust-design models can account for temporary emigration and the effects of individuals becoming unavailable for capture (Kendall et al. 1997).

Arctic ground squirrels occur in a wide range of habitats, from boreal forest to shrub and alpine tundra (Chapter 2), however, habitat suitability differs between these habitats. Previous studies have indicated that generally higher survival occurs in more open alpine areas where visibility is greater and predation risk lower than in the forest (Gillis et al. 2005a; Donker 2010). However, arctic ground squirrel habitats are in transition, and as climate warms, woody species are increasing in density and extending their range into tundra (Sturm et al. 2001; Tape et al. 2006; Danby and Hik 2007; Myers-Smith et al. 2011). Changes in habitat distribution have the potential to have considerable impact on arctic ground squirrels and their ecosystem role as major agents of disturbance via burrowing activity and as prey species (Price 1971; Reid et al. 1997; Prugh 2005), and it is becoming increasingly necessary to accurately monitor population trends (Chapter 2).

Although arctic ground squirrels hold individual territories, they are typically central place foragers, with colonies located around permanent burrow systems (Carl 1971; Watton and Keenlyside 1974; Lacey et al. 1997). Home ranges of females in the boreal forest were estimated to be 3ha for 95% of utilisation, suggesting relatively restricted movements (Hubbs and Boonstra 1998). Foraging is also generally thought to occur locally, within 30m of burrows (Batzli and Sobaski 1980), although longer distance movements are not uncommon (e.g. Gillis et al. 2005b).

There is evidence of temporary habitat associations in this species, which has been overlooked when estimating survival. Temporary, less extensive burrow systems are well-described in arctic ground squirrels and may be associated with transient occupancy (Carl 1971). These temporary burrow systems are generally thought to be associated with poorer quality habitat (Batzli and Sobaski 1980). If the extent of these temporary associations does vary between habitats, this would bias comparisons of survival between habitats and weaken inferences made from these estimates.

Both habitat suitability and seasonal life history events have the potential to affect the extent of temporary habitat associations. Habitats which provide poor conditions for survival may have greater likelihood of individuals showing temporary associations (e.g. Rémy et al. 2011). This may occur as a result of habitat being insufficient to provide for all needs of individuals, because there a fewer territorial barriers to new immigrants and because new immigrants are less likely to settle in poor suitability habitat. Even where habitat is insufficient to maintain a resident population, temporary associations may still occur as a result of use of poor quality habitat as movement corridors (Haddad and Tewksbury, 2005). Variation in fidelity to a single location will be influenced by seasonal requirements. These changes may be seen with respect to forage, mating opportunities, safety from predators or abiotic factors such as extreme weather events. Temporary seasonal movements are more commonly described in large mammals (e.g. Festa-Bianchet 1988, Zweifel-Schielly et al. 2012), but there are implications for smaller mammals as well (e.g. Palmer and Woinarski 1999; Harding 2000).

I assessed the extent of temporary habitat association in adult female arctic grounds squirrel populations inhabiting three different habitats associated with a shrub to tundra ecotone. I assessed how differences in habitat suitability might affect temporary movements and whether these behaviours varied seasonally. I developed the following four predictions for our hypothesis that habitat suitability and life history events influence the pattern of temporary habitat associations.

1. Arctic ground squirrel populations exhibit temporary associations with habitat. We predicted there will be greater support for models incorporating temporary habitat associations than those assuming permanent adult association.
2. Temporary associations are greater in lower quality habitats with lower survival as a result of lower fidelity to poorer quality habitat and reduced barriers to immigration. Habitats with low survival were therefore expected to have greater transience and greater temporary emigration and immigration.
3. Temporary movements will cause models omitting these movements to underestimate survival. These low biases would be greatest in poor suitability habitat. Differences in survival estimates between temporary association

models and permanent association models were predicted to be greatest in habitats with greatest temporary associations.

4. Temporary movements would be greatest subsequent to weaning of juveniles, as adult females would be less strongly tied to the safety of a given burrow system.

Methods

Trapping

Populations of arctic ground squirrels were studied in an alpine valley in the Ruby Range, south west Yukon, (61°21′ N, 138°27′ W). Variation in survival and temporary movements were considered by comparing sites across an elevational gradient from 1450m to 1950m above sea level. Robust-design capture recapture trapping was used to ascertain survival on eight 200m by 200m (4ha) grids within shrub (three grids), shrub-tundra (one grid) and tundra habitat (four grids). Trapping sessions were conducted in June, July and August in 2008 and 2009 and June in 2010. Each grid consisted of 25 Tomahawk traps (Tomahawk live trap llc, Hazelhurst, USA) set with 50m spacing between traps and trapped five times within a two week period at the start of each month. In June 2010 adverse weather required the trapping session to be conducted over a longer period. Squirrels were individually marked with Monel no.1 tags on each ear (National Band and Tag Co, Newport, USA). Data were pooled across grids within a given habitat. Only adult females were included in this analysis as these were deemed likely to show least temporary habitat associations and therefore provide a conservative estimate of transience in this species. Techniques were approved by the University of Alberta Animal Care Committee and followed the guidelines of the Canadian Council on Animal Care.

Survival estimation

Survival was estimated for adult females in each habitat using transience and temporary emigration models. Data were pooled across grids within a given habitat. Goodness of fit (GOF) tests were performed on the data pooled across habitats and pooled within a primary session using the program RELEASE (Burnham et al. 1987) implemented in program MARK (White and Burnham 1999). Goodness of fit tests were used to assess whether models incorporating transience (Test 3 SR2) and temporary emigration (Test 2) should be considered in subsequent analyses.

Initially, data were analysed using the transience approach of Hines et al. (2003) for survival estimation from robust design data. This approach uses only known residents to estimate survival. Known residents are those whose trapping history shows that they have a long-term association with the habitat. Separate from these are the unknown resident class, which should include all individuals which only have a single short-term association with the habitat (transients) and those that cannot be distinguished from transients due to their capture history. The transience rate can then be estimated based on model parameter estimates associated with the differing unknown residency group and resident survival (Clavel et al. 2008).

To implement these methods data were reduced from a robust design to an open capture design consisting of only primary sessions. Data from secondary sessions were used to assign individuals to a group of either known residents or unknown residency. Individuals caught only once within a primary trapping session (month) and those caught only twice in succession were considered of unknown residency and all others were considered resident.

Several assumptions were made regarding the model. Monthly active season (June to September) survival was assumed to differ from overwinter (September to June) survival. Captures in September were removed from the transience structured analysis as females are known to enter hibernation during this month and hence become unavailable for capture. Transience rates (π) of the unknown residence class were assumed to be constant over time and between habitats. The global model for the transience model structure allowed survival to be affected by the year and habitat, and allowed for monthly temporal variation in active season survival. Probability of capture was allowed to vary over time, between habitats and between known residents and the unknown residency class. A bootstrap GOF test was implemented to assess fit of the global model.

Probability of capture was explored using all potential combinations of parameters to assess whether the key factors determining probability of capture could be fixed in subsequent models. Survival was examined using eight models considering parameters affecting survival only. Factors affecting survival were then explored under this structure. Relative support for models containing all possible combinations of variation in survival between time, habitat and year were assessed using corrected Akaike's Information Criterion (AICc, Burnham and Anderson 1998).

Approximations of transience rates were then made following the approach of Clavel et al. (2008). The best model and one allowing variation in transience by habitat were re-run using a log link function. This allowed approximation of transience rates of the unknown class in each habitat. From these data, approximate proportions of individuals caught deemed transient were estimated. As abundance estimation was not conducted in this study, only an approximation of proportion of the population considered transient is obtained in each habitat. Capture probabilities did not differ substantially between habitats, so the estimation of proportion of individuals transient was considered valid.

Temporary emigration was considered using the same model structure selected for the best transience model. These models assumed no transient individuals (with solely a single short-term habitat association), but allowed temporary emigration and immigration such that individuals may temporarily leave the habitat and return. To execute this, a robust design model based on the Huggins models (Huggins, 1989, 1991; White 2008) was implemented using the program MARK. Transience was also incorporated in to this model. Likelihood ratio tests were used to compare nested models to consider whether there was significant temporary emigration, and whether emigration was Markovian such that temporary emigration probability (γ') is not equal to temporary immigration probability (γ'') or random ($\gamma'=\gamma''$). The potential for transience structure under the robust design was also tested.

Temporary emigration models often suffer from unidentifiable emigration parameters if they vary temporally (Kendall et al. 1997). Therefore emigration was classified into two distinct periods given prior knowledge of the system. It was assumed that July to September represents the period where individuals may become unavailable for capture. This was likely for two reasons; individuals start to enter hibernation (apparent emigration) and this is the post breeding and weaning period where small mammals often become less territorial and less strongly associated with a given area (Wolff 1993). In the model, this was considered a seasonal effect influencing emigration. Once the models had been reduced according to the results of likelihood ratio tests eight models remained (Table 3.2). Corrected Akaike's Information Criterion AICc was used to consider the relative fit and parsimony of models. Survival and temporary emigration rates were retrieved from this model. AICc weights were used to assess the support for temporary emigration and immigration.

Results

Goodness of fit

Data were relatively sparse for effective testing for transience (Test 3.SR2). In some months, transience was a clear possibility (χ^2 2.1-3.5, d.f=1, p~0.1 in three of seven months); other months had insufficient data for effective testing; a transience model was therefore considered. Results of Test 2 gave very strong indications of temporary variation in availability for capture (χ^2=31.74, d.f.=6, p<0.0001).

Transience structure: model selection

The global transience model provided an acceptable fit to the data (GOF test $\hat{c}$=1.02, p=0.531), therefore no adjustments were made for overdispersion. There was strong support for transience in this model (χ^2=19.077, d.f.=3, p=0.0003). When selecting between capture probability parameterizations, the full parameterization and a structure containing residency group and temporal (monthly) variation in capture probability had considerably more support as the structure for capture probability than other parameterizations (ΔAIC_c between second best model and third best model 6.5, AIC_c weight (w_i) of the third model < 0.01). Of the two best models, the simpler structure was selected, although the difference in support between models was more marginal (ΔAIC_c=0.9).

Transience structure: Transience rates and survival estimation

The data best supported a model where active season survival was determined solely by habitat (Table 3.1). Habitat appeared to be a key factor explaining variation in survival (w_+=0.83), whereas interannual and seasonal variation during the active season were less strongly selected across the model set (w_+=0.25 and w_+=0.29 respectively). Survival was high in tundra and shrub habitats but appeared much lower in shrub-tundra (Fig. 3.1).

Variation in transience rates between habitats within the unknown category were not supported (ΔAICc=3.46) and therefore not used in survival estimation. However, variation in transience rate of the unknown class between habitats was evident (Fig. 3.2a) and when considered in conjunction the proportion of captured individuals considered transient (Fig. 3.2b), suggested that the proportion of transient individuals caught in each habitat may be quite different between habitats (Fig. 3.2c). A much higher proportion of transient individuals were caught in shrub-tundra habitats. Estimates of transience rates of the unknown class were associated with large errors;

however, when considered in conjunction with differences in proportion of individuals in each habitat attributed to the unknown class, they demonstrated considerable variation in transience between habitats (Fig. 3.2c).

Robust design, temporary emigration model selection

In the temporary emigration model, transience structure was no longer supported ($\chi^2=1.286$, d.f.=2, p=0.53), however there was very strong support for a temporary emigration parameterization ($\chi^2=117.752$, d.f.=2, p<0.0001). Temporary emigration was Markovian rather than random ($\chi^2=34.879$, d.f.=2, p<0.0001) such that probabilities of emigration were not equal to immigration probabilities. A greater probably of temporary emigration than temporary immigration was observed (Fig. 3.3).

Robust design, temporary emigration: survival estimation

As seen in the transience model, habitat was the most strongly supported source of variation in survival across the model set ($w_+=0.81$). Both temporary emigration and immigration showed strong seasonal variation ($w_+>0.99$ in both cases) and were higher in the later part of the season (July to September) than in the interval encompassing overwinter, emergence and the subsequent June to July period (Fig. 3.3).

Comparisons of model survival estimates

All models displayed similar qualitative relationships between habitat and survival (Fig. 3.1). The transience model showed the less difference in survival estimates between shrub-tundra and shrub and tundra than other models. As might be expected, removal of the transience effect from the transience model or temporary movements from the robust design model caused a reduction in survival estimates (Fig. 3.1).

Discussion

Temporary habitat associations appear more common than previously discussed for arctic ground squirrels. This was demonstrated by the high levels of support for temporary emigration and transience models relative to more static models. Both short term transient associations with habitats and temporary immigration and emigration appear common in these populations. Omission of these processes appeared to result in biases in absolute and relative estimates of survival between habitats.

Levels of transience were greatest in the shrub-tundra, where lowest survival was observed. Although this trend in shrub-tundra represents results from a single population, it appears that levels of transience are greater in the transitional habitat compared with tundra or shrub. However, perhaps most important result is the association between low survival and high transience. Several mechanisms could contribute to this trend. First, in a low-survival habitat where individuals are regularly lost from territories there may be fewer territorial obstructions to movements from non-resident individuals, therefore more non-residents may use these habitats as corridors or may enter to assess suitability. Second, transients may represent individuals in poorer condition. These individuals may be excluded from habitats associated with higher survival. Increasing evidence also suggests individuals born in poor habitat may make worse settlement decisions, due to differing prior experiences of habitat quality (Davis and Stamps, 2004). In general, individuals may be less likely to settle or more likely to emigrate from less desirable habitats (Bonte et al. 2004; Lin and Batzli 2001) resulting in a negative association between survival and transience rates. Finally, social benefits of territoriality may result in increased survival (McCormick and Meekan 2007) but exclude new immigrants.

A key concern when comparing survival between habitats where levels of transience differ with conventional models is that greater use of a habitat by transient individuals may cause survival estimates to be biased low relative to other habitats. This is suggested when comparing estimates under the transience and no transience models where differences in survival between shrub-tundra and other habitats are greatest when models without temporary movements are used. In addition, population density estimates may be inflated by inclusion of such transients.

Temporary emigration and immigration were greater between July and September than during the rest of the year (which encompasses the period from adult emergence from hibernation until juvenile emergence from natal burrows). The period from July to September represents the weaning and dispersal period for juveniles (Green 1977; Byrom and Krebs 1999), and may also represent a period of less strong habitat associations for adult females. Juvenile arctic ground squirrels are at high risk from both predatory attack (Byrom and Krebs, 1999) and also experience infanticide

(McLean 1983). Once juveniles have grown larger their risk of predation and infanticide may be reduced. As juveniles are weaned there may be fewer requirements for adult females to remain near their burrows to protect young and this may facilitate a phase of greater mobility for adult females (e.g. Madison 1978). For example, increased home range post-lactation has been documented in adult female Franklin’s ground squirrels (Choromanski-Norris et al. 1989). Removal of the spatial constraint imposed by dependent young may allow arctic grounds squirrels to move and track changing habitat suitability or explore opportunities for gaining territories in more favourable habitat to a greater extent. This may be reflected in higher temporary emigration and immigration rates.

Other life-history events may also affect apparent temporary emigration. Individuals entering hibernation early may become temporarily unavailable for capture, whilst still associated with the focal area for monitoring, potentially causing an underestimation of capture probability or survival toward the end of the active season. The combination of life-history and ecological considerations and ecological processes that may cause more temporary habitat associations requires that these models are addressed more commonly in such species.

Temporary habitat associations may be a result of seasonal variation in habitat quality. Strong seasonal variation in forage is seen in the northern alpine and may drive temporary habitat associations. Temporary movements may be more common in habitats which show strong seasonal variation in resources (Kirk et al. 2008), such as high latitude environments. Adult migration as a response to temporal variation in habitat quality has been described in many species including in other scurids (Lurz et al.

1997; Wauters et al. 2005). The fact that dispersal has been documented in adults as well as juveniles for arctic ground squirrels (Lacey 1991) provides further support that mobility is high despite strong associations with burrow systems and that temporary movements also may be quite common.

In addition to strong seasonal variation in habitat experienced during the active season for arctic ground squirrels, there may also be high variation in resource requirements. Upon emergence from hibernation, habitat is largely snow covered, and forage relatively unavailable. Males are thought to consume caches prior to emergence and lose considerable mass early in the season during breeding as they mainly live off energy reserves (Buck and Barnes 1999). Females, however, maintain mass during this period and may be relying more on the little available vegetation, such as buds from shrubs, which may provide important forage (Batzli and Sobaski 1980). As the season progresses, forage becomes more plentiful, the relative value of forage in different areas is altered and habitats that provide safety for young may become more important. Towards the end of the active season fatty acids and foods suitable for caching may be critical components of diet and nest building materials may also be important (Gillis et al. 2005b; Frank et al. 2008); the need to find foods suitable for caching and for obtaining sufficient fatty acids may influence habitat use. Finally, adult females have been observed to select areas for hibernation with warmer burrow temperatures than other demographic groups and this may influence associations prior to hibernation (Buck and Barnes 1999).

Burrowing mammals might be assumed to be relatively fixed in their habitat use, constrained by the need for burrow refuges. However several burrowing species have been documented to use multiple burrow systems (e.g. burrowing bettong, Finlayson and Moseby 2004; wombat, Evans 2008; pygmy rabbit, Sanchez and Rachlow 2008), woodchuck (Swihart 1992). In particular, this may be facilitated when available burrows outnumber individuals or social groups (Evans 2008). The high effort required to ascertain whether individuals use multiple burrow systems may result in relatively low rates of detection of this phenomenon. Temporal variation in space use can be associated with timing of life history events, perhaps the most common being mating, which can either increase space use (Sanchez and Rachlow 2008) probably to aid mate finding, or cause decreases in space use (Moro and Morris 2000) associated with increased territorial defence. For female burrowing mammals, vulnerability of young may increase with distance from burrow refuges, so movements away from these refuges may be constrained until young are independent. When spatial variation in resources is combined with temporally varying needs, advantages of temporary movements may be high.

Qualitatively, all models in this study suggested survival was lowest in shrub-tundra and highest in tundra and gave support to the hypothesis that higher visibility in tundra resulted in highest survival rates. Quantitative predictions, however, differ substantially between models. In general, the analogous models without temporary movements produce lower estimates of survival than those with temporary movements. This study suggests that the presence of transient individuals and temporary changes in habitat associations may be common even for a central place forager such as the arctic ground squirrel which is normally thought to be associated with a burrow over a relatively long time period. By ignoring temporary movements there is a clear potential for bias in survival parameters for this species.

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Table 3.1. Model selection for survival estimation of arctic ground squirrels under the transience model. Survival (Φ) was allowed to vary by combinations of habitat (h), year (y) and month during the active season (t). Transience rate of the unknown residency class (π) was fixed across habitats, months and years. Probability of capture (p) varied between monthly trapping sessions (t) and between known residents and individuals of unknown residency (r).

Model	AICc	ΔAICc	AICc Weights	Num. Par	Deviance
Φ_{h},π.,p_{tr}	447.8	0.0	0.44	9	168.6
Φ_{th},π.,p_{tr}	449.5	1.7	0.19	10	168.1
Φ_{hy},π.,p_{tr}	450.0	2.2	0.15	10	168.6
Φ,π.,p_{tr}	450.9	3.1	0.09	7	176.1
Φ_{thy},π.,p_{tr}	451.7	3.9	0.06	11	168.1
Φ_{t},π.,p_{tr}	453.1	5.2	0.03	8	176.0
Φ_{y},π.,p_{tr}	453.1	5.2	0.03	8	176.0
Φ_{ty},π.,p_{tr}	455.2	7.4	0.01	9	176.0

Table 3.2. Comparison of models where habitat affects different seasonal components of survival of arctic ground squirrels under the robust design model.

Survival	Emigration	Immigration	Capture probability	AICc	ΔAICc	AICc Weight	Num. Par	Deviance
Habitat	Season	Season	Time	2472.38	0.00	0.81	12	2492.29
Constant	Season	Season	Time	2475.25	2.88	0.19	10	2499.30
Habitat	Constant	Season	Time	2492.37	19.99	0.00	11	2514.35
Habitat	Season	Constant	Time	2494.02	21.64	0.00	11	2516.01
Constant	Constant	Season	Time	2494.56	22.19	0.00	9	2520.68
Constant	Season	Constant	Time	2497.02	24.64	0.00	9	2523.13
Habitat	Constant	Constant	Time	2502.38	30.00	0.00	10	2526.43
Constant	Constant	Constant	Time	2505.06	32.69	0.00	8	2533.23

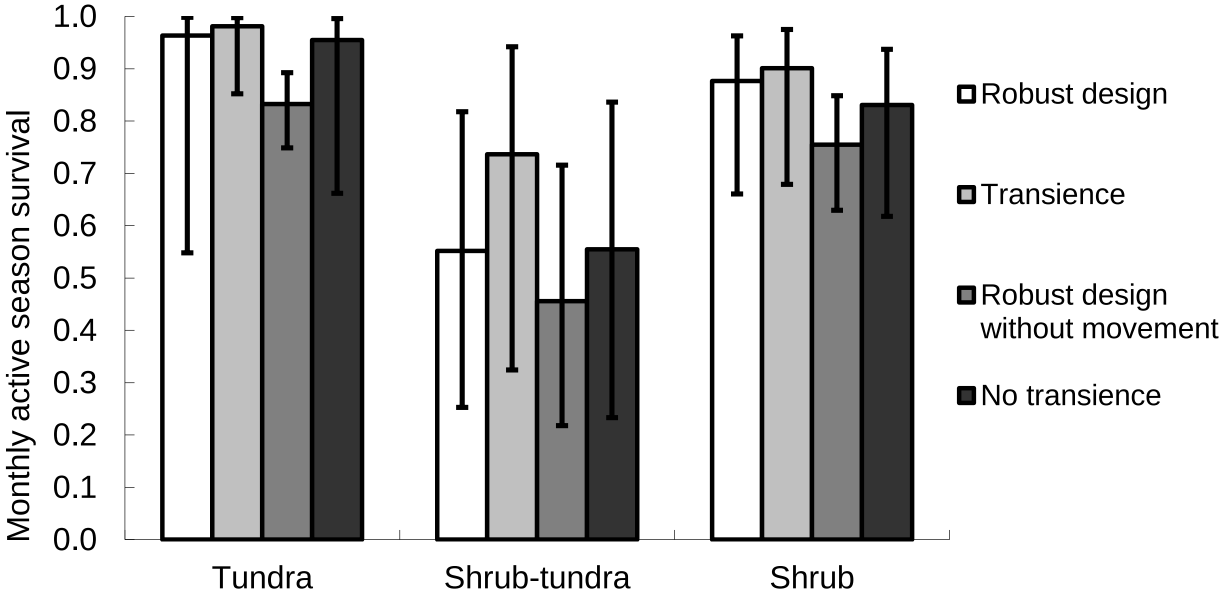

Figure 3.1. Best estimates of adult female arctic ground squirrel active season survival under robust design (temporary movements), transience, robust design in the absence of temporary movements and transience model without transience structure. Values are mean ± 95% confidence intervals.

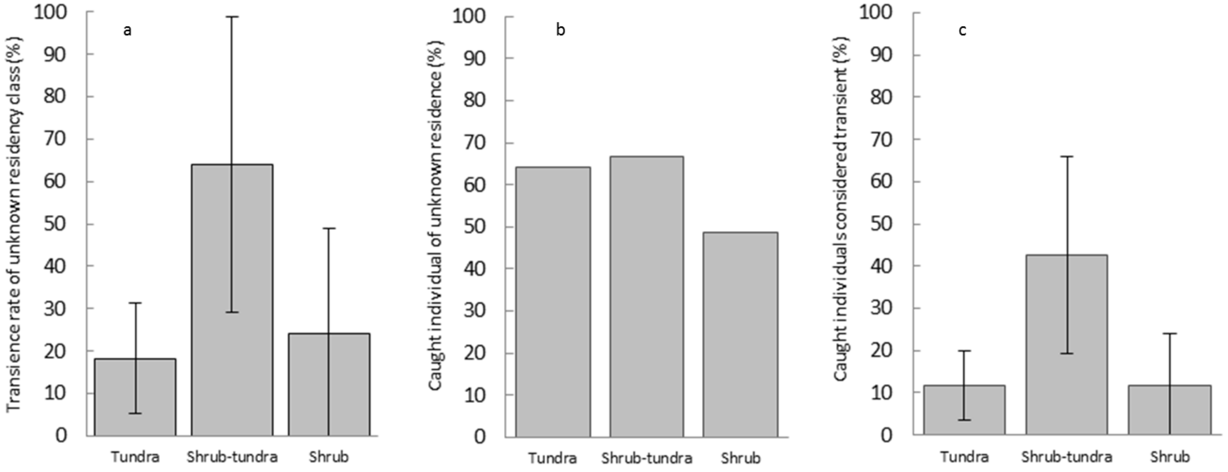

Figure 3.2. Transience rates for arctic ground squirrels of unknown residence (a), proportion of all individuals trapped with unknown residence (b), and transience rate of all trapped individuals (c) across three habitats varying in shrub cover. Values are mean ± 1 SE.

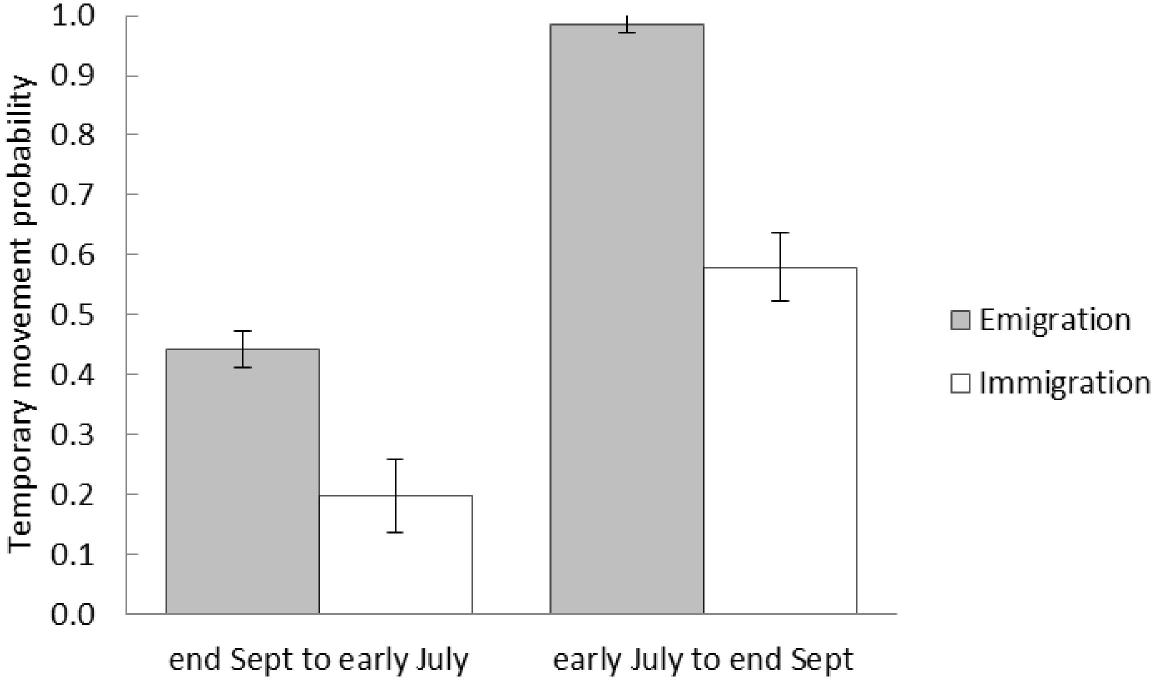

Figure 3.3. Probability of temporary movements of arctic ground squirrels during hibernation and early in the active season and from early July to end September. Values are mean ± 1 SE.

Chapter 4

Arctic ground squirrel habitat suitability across a gradient of shrub tundra: contrasting assessments from population and behavioural models

Introduction

Shifting habitat distributions have the potential to cause global and local extinctions and allow expansion of wildlife in to new areas (Burns et al. 2003; Thomas et al. 2004). One such shift is occurring as a result of encroachment of woody species to higher altitudes and more northerly latitudes, which may transform habitat for many northern mammals. Warming climates are associated with increases in the density and extent of boreal forest species and canopy forming shrubs (Myers-Smith et al. 2011; Gottfried et al. 2012). These changes will significantly modify the physical structure and visibility of alpine meadows and tundra habitats from very open landscapes to landscapes that are much more visually obstructed. For species which rely on high visibility for predator detection, this could greatly reduce habitat suitability.

To project species' response to changing habitat there must be mechanisms for quantifying habitat suitability. Models have been developed in a number of disciplines; population ecologists focus on combinations of occupancy, density and survival (Jorgensen et al. 1998); indices of condition have provided further means of assessing suitability from individuals in a population (Johnson 2007); while behavioural studies often focus on metrics associated with foraging and marginal value theorem (e.g Searle et al. 2007). Increasingly, measures such as giving-up density are being used to infer habitat suitability (e.g. Morris and Davidson 2000; Vickery et al. 2011).

Whilst there has been considerable discussion concerning how to best assess habitat suitability using population data (Van Horne 1983), less attention has been paid to congruence of indicators between population biology and behavioural ecology or individual based metrics of suitability. Inconsistencies between analogous measures of suitability made at population and individual levels have been demonstrated (Pidgeon et al. 2006). Reconciliation between these disparate measures of habitat suitability and between perspectives from subdisciplines of ecology will lead to more accurate and detailed assessment and understanding of habitat suitability.

Arctic ground squirrels (*Urocitellus parryii*, Osgood 1900) are a widely distributed species found across arctic and subarctic regions of Canada, Alaska and Siberia (Helgen et al. 2009, Chapter 2). They can reach high local abundances, occur in a wide range of habitats and affect ecosystems as agents of disturbance through extensive burrowing activity (Banfield 1974; Hall 1981; Price 1971). They act as prey items, predators and grazers and can cause local fertilization of soils (Bailey 1975; McKendrick et al. 1980; Poole and Boag 1988; Boonstra et al. 1990; O'Donoghue 1994; Reid et al. 1997; Prugh 2005). Surprisingly little attention has been directed at understanding what determines habitat suitability for this species and projecting how distribution will change with climate warming (Chapter 2).

Arctic ground squirrels appear to rely heavily on open landscapes for predator detection. Predators have an important role in population processes and predation is a major source of mortality in this species (Hubbs and Boonstra 1997; Byrom et al. 2000; Karels et al. 2000). Boreal forest may be poor habitat due to high predation risk (Hik et al. 2001; Gillis et al. 2005). Increased predation risk in the boreal relative to more open tundra could occur both because of greater densities of predators and reduced ability to detect predators (Hubbs and Boonstra 1997; Hik et al. 2001; Gillis et al. 2005; Donker and Krebs 2011). Landscapes where vegetation obstructs visibility may therefore increase predation risk and reduce habitat suitability for arctic ground squirrels.

Most studies related to habitat suitability for arctic ground squirrels have focused on population level inferences. However, many authors have criticized the use of population density alone as an indicator of habitat suitability (Van Horne 1983; Bock and Jones 2004) because density can provide a misleading indication of habitat quality where source sink dynamics occur, in the presence of ecological and perceptual traps and in territorial species, where vital rates may vary spatially in a different manner to density (Mosser et al. 2009; Heinrichs et al. 2010; Patten and Kelly 2010). Many of these spatial phenomena are more common in areas where habitats are changing (Battin 2004; Bock and Jones 2004). Incorporation of survival into population models may overcome many of the limitations associated with density alone.

Giving-up density (GUD) is a behaviourally-derived index of the costs of foraging in a habitat and as such should provide a reliable indication of habitat suitability. GUD provides an index of the sum of the energetic, predation and missed opportunity cost associated with foraging (Brown and Kotler 2004). Individuals at greater risk of predation should experience higher costs associated with foraging and therefore leave foraging patches earlier and have higher GUDs. While certain components of GUD such as predation risk, that have received greater attention, should provide indices of suitability compatible with those at the population level, others may not (Fig. 4.1).

In this chapter I use survival and density estimates, giving-up density and individual mass as indications of habitat suitability for adult female arctic ground squirrels. Using these indices I compare assessments of habitat suitability across a shrub-tundra ecotone using population (survival and density), behavioural (giving-up density) and individual condition metrics. I hypothesised that open tundra would have higher suitability than more visually obstructed shrubby habitats and that either shrub or shrub-tundra would be lowest suitability, depending on the extent of benefits derived from cover for avoiding detection and from visibility detecting predators in these more visually obstructed habitats. I predicted that higher suitability habitats should support higher survival and density at the population level. I predicted that cost of foraging should be lower in higher suitability habitats and therefore expected lower GUDs. I also expected that high suitability habitat should be associated with better condition individuals of higher mass. I used these individual and population-level estimates of habitat suitability to investigate how ground squirrels could respond to vegetation changes in this alpine tundra landscape.

Methods

Study site

Populations of arctic ground squirrels were studied across an elevational gradient of 1450m to 1950m above sea level (A.S.L.) in the Ruby Range (61°21'N, 138°27'W), SW Yukon, Canada. Lowest elevation shrub habitats were associated with dense willow shrub (*Salix richardsonii* and *S. pulcra*), reaching over 2m in height and forming dense canopies. Intermediate elevation shrub-tundra (~1600m) was associated with more patchy distribution of willow shrub, rarely exceeding 1m in height. At the highest altitudes (~1700-1950m), alpine tundra had less than 10% cover of canopy-forming shrubs.

Trapping

Capture recapture trapping following the robust design was performed over eight 200m by 200m (4ha) grids to ascertain survival and density. Within each grid, Tomahawk traps (Tomahawk Live Trap co., Hazelhurst, WI, USA) were set with 50m spacing between traps. Trapping was conducted in June, July, August and September in 2008 and 2009 and June only in 2010. Each grid was trapped 5 times within a two week period at the start of each month. June 2010 was an exception, where the trapping session was conducted over a longer period because of adverse weather; therefore this data was not used for density estimation. Four grids were considered tundra, one was considered a transitional habitat between shrub and tundra (shrub-tundra), and three were considered shrub. Upon capture, squirrels were individually marked with Monel no.1 tags (National Band and Tag co., Newport, KY, USA). To aid identification at a distance, individuals were also given unique dorsal alpha numeric marks using hair dye (No. 52. Black Pearl, Hydrience, Clairol). Data were pooled across grids within a given habitat.

Line of sight

Line of sight was estimated on each grid at twenty-five locations across the grid each with 50m spacing. Percentage of a 1m by 1m board visible from distances of 5, 10, 15, 20 25 and 50m from an eye line of 20cm above ground was estimated across each of four cardinal directions. There measurements were used to compare line of sight between habitats at a range of distances.

Survival estimation

Based on model development outlined in Chapter 3, a robust design model incorporating temporary emigration based on the Huggins models (Huggins 1989; 1991; White 2008) was used to estimate survival. This conditional likelihood model can be used to estimate survival, probability of capture (assumed in this case to be equal to probability of recapture), temporary emigration and temporary immigration probabilities from robust design trapping data. Additionally, abundance is estimated as a further derived parameter from probability of capture and capture frequencies. The model was implemented using the program MARK (White and Burnham 1999). The global model structure incorporated the effect of year and habitat on survival, and allowed for monthly temporal variation in active season survival. Monthly active season (June to September) survival was assumed to differ from overwinter (September to June) survival. Probability of capture was allowed to vary over time. Emigration was Markovian; based on previous model development, two distinct periods of differing temporary movement probabilities were identified, July to September and end September to early July. In the model, this was considered a seasonal effect upon emigration. Corrected Akaike's Information Criterion (AICc) was used to consider the relative likelihood and parsimony of models. Whether the effect of habitat on survival was mediated through active season or overwinter survival or a combination of the two was then assessed. Derived abundance estimates were calculated from this model, estimates, and their associated standard error were corrected for the area trapped to provide density estimates. July densities reflected peak squirrel abundance in the valley and were therefore used for habitat comparisons.

Giving-up density

GUD was estimated for individual adult female squirrels using remotely monitored feeding trays comprising 8g of quartered peanuts mixed randomly throughout four litres of sand. Feeding trays were monitored using two cameras and video footage was recorded to DVR for later analyses (IR bullet camera, 420 TVL and 4 channel DVR, Zurich Lock and Key, Illinois, USA). Footage was also transmitted to an observer at 300m distance and away from sight of the foraging tray via radio-transmitter (Spytronic, Quebec City, Canada).

GUD was calculated as the mass of peanuts remaining after a foraging bout had ended. Foraging bouts were deemed to have ended when a squirrel had left the foraging tray without returning for five minutes. The procedure relied on the decrease in density of peanuts in sand as more peanuts were consumed, such that a decreasing energetic rate of returns was expected as the tray was depleted. A high GUD implied an individual had left while energetic returns were still high, whilst a low GUD suggested peanuts had been consumed down to a much lower rate of return. GUD therefore a GUD represents a titration between the cost of foraging in a habitat and the energetic rate of return from foraging. A low GUD implies a lower cost of foraging (Brown and Kotler, 2004). GUDs were compared between habitats using ANOVA. GUD was log-transformed such that data did not differ significantly from a normal distribution at α=0.1.

Seasonal mass trends

Seasonal mass trends from mid-June to mid-September were recorded from trapping data. A linear mixed model considering the effect of time of year (date), habitat and year upon adult female Arctic ground squirrel mass; squirrel identity was included as a random effect. Mass data was log-transformed to improve conformity of errors to a normal distribution. Analysis of variance was used to test for seasonal trends in mass, and variation in mass between habitats and years. Analyses were conducted in Program R (version 2.13.0).

Results

Line of Sight

Line of sight differed substantially between all habitats (Fig. 4.2). Tundra sites were associated with highest visibility across all distances. Shrub sites consistently had less than half the visibility of tundra sites. Shrub-tundra showed intermediate but distinct visibility compared to the two other habitats. Visibility initially declined rapidly with as distance increased; as distances became greater the rate of visibility decline reduced considerably to a near-plateau. The visibility at this plateau may represent long-distance visibility in each habitat.

Survival and density

Habitat appeared be an important determinant of survival (w_+=0.81, Table 4.1), considerably more so than temporal effects associated with interannual or seasonal variation in survival (w_+=0.25 and w_+=0.29 respectively). Habitat had greater effects on active season than overwinter survival (Table 4.2). Between habitats, survival was greatest in tundra and considerably lower in the transitional shrub tundra habitat than in tundra or shrub (Fig. 4.3).

Arctic ground squirrels occurred at substantially greater densities in alpine tundra than in shrubbier habitats. Densities of adult females were greatest in alpine tundra, intermediate in shrub and lowest in shrub tundra in both 2008 and 2009 (2.04±0.09, 1.14±0.07 and 0.80±0.12 females ha^{-1}, respectively, in 2008, and 2.06 ± 0.09, 0.89 ± 0.08 and 0.53 ± 0.08 in 2009). Interannual variation in density was considerably greater in shrub-tundra than in tundra or shrub (Fig. 4.4). Density and survival were positively correlated (Fig. 4.4).

Giving-up density

Habitat type had a significant effect on GUD (ANOVA, $F_{2,8}$ = 7.04, p = 0.017). Shrub-tundra and tundra had lower GUDs than shrub habitats (Tukey post-hoc test $p < 0.05$, Fig. 4.5a). GUDs in shrub-tundra and tundra habitats did not differ significantly, however lack of statistical significance may be a result of low sample size. When considering all ages and demographic groups, GUD showed the same differences between habitats and lower GUD in shrub-tundra and tundra than in shrub, these were the same qualitative trends as seen for adult females (ANOVA, $F_{2,19}$=18.25 , in Tukey post-hoc tests for pairwise differences $p < 0.05$ between shrub and other habitats, Fig. 4.5b).

Seasonal mass trends

As expected, mass of adult females increased throughout their active season (ANOVA, $F_{1,451}$ = 327.9, $p < 0.0001$, Fig 4.6). However, significant variation in mass was evident between habitats (ANOVA, $F_{2,451}$ = 22.7, $p < 0.0001$ Fig. 4.6); mass was substantially lower in shrub habitat than in tundra or shrub-tundra (Tukey post-hoc comparisons, $p < 0.001$). Shrub-tundra also had significantly higher mass than tundra (Tukey post-hoc comparison, $p = 0.003$). Masses in 2009 were significantly higher than in 2008 (ANOVA, $F_{1,451}$= 27.99, $p < 0.0001$).

Discussion

This study has two major findings. First, habitat suitability differs between habitats across a shrub tundra ecotone, with shrub-dominated habitats being less suitable than open tundra. Second, indices of habitat suitability at the population and individual level do not always agree. Results indicate female survival rates, densities and individual masses were higher and costs of foraging were lower at tundra versus shrub sites. These individual- and population- level data show that shrub habitat was less suitable than tundra habitat. However, trends in the intermediate habitat, shrub-tundra, demonstrated that indications of habitat suitability from the population and behavioural levels were contradictory (Table 4.3), and need to be integrated to achieve a full understanding of habitat quality.

Survival and density

Densities and survival of adult females in tundra were comparable with the estimates of density previously reported in the alpine from adjacent populations (Gillis et al. 2005). Densities in late July to early August were between 0.3 and 0.9 adult females ha^{-1} according to Gillis et al. (2005). Density in this study in early August was 1.0 females ha^{-1} in 2008 and 0.8 females ha^{-1} in 2009. Survival in tundra was also similar to Gillis et al. (2005) which considered return rates of adult females and reported survival of approximately 87% over a 2 month period. In this study, survival over a 2 month period in the active season was 93±11% in the tundra.

Both survival and density were highest in tundra, which provides very strong support that this is the highest suitability habitat. This finding also agrees with previous studies which have suggested reduced predation risk in open alpine tundra contributes to lower stress (Hik et al. 2001), higher survival and density (Gillis et al. 2005; Donker and Krebs 2011) and selection for tundra over treed areas at large scales (Barker and Derocher 2010). These differences support the hypothesis that shrub encroachment will negatively impact arctic ground squirrel populations.

Shrub supports considerably lower densities than tundra, but has only marginally lower monthly survival. One likely possible reason for this pattern is that density dependence is depressing survival to a greater extent in tundra than in shrub. Density dependence in population dynamics has been well described and can affect both survival and reproduction in arctic ground squirrels (Karels and Boonstra 2000). Most important may be the previously described density dependence in overwinter survival. Shrub-tundra has both low survival and low densities and is a clear candidate for the lowest suitability habitat when considering population data alone. The apparent difference in suitability between shrub and shrub-tundra is greater than might be expected given both have relatively high levels of visual obstruction (Fig. 2) and is unlikely to be explained by density dependence unless Allee effects (Courchamp et al. 1999) affect shrub-tundra populations. Indeed, Allee effects are possible in this system where predator detection and alarm calling are heavily employed and may less be effective at low population density.

Giving-up density and mass

GUD trends suggest that the costs of foraging are lower in shrub-tundra and tundra relative to shrub. If we expand these results to the entire population (Fig. 4.6b) it appears that shrub-tundra has the lowest GUDs, with tundra having marginally greater GUD and shrub much higher. Consistent results were observed for adult females and in the population as a whole. Trends in mass were consistent with the notion that GUD reflects the intensity at which individuals are willing to forage in a habitat, such that habitats with high GUD have lower mass individuals. If real or perceived predation risk is the main driver of GUD in this system, there are surprisingly large differences between shrub-tundra and shrub habitats, both of which had substantially obscured visibility (Fig. 4.6).

Habitat suitability from multiple indices

I found differing indicators of habitat suitability using individual and population-based methods for the shrub-tundra habitat. Shrub-tundra had lower survival and density than all other habitats but very low GUD and high mass. Conversely, shrub had survival and densities intermediate to shrub-tundra and tundra but very high giving up densities and high mass. These trends in shrub and shrub-tundra relative to tundra require further examination.

The most likely cause of the discrepancy in the more shrubby habitats is the interaction between components of GUD, population processes and habitat (Fig. 4.1). Habitat properties, population processes, the state of individual squirrels and interactions between the two could cause apparent inconsistencies between indicators of habitat suitability at the population and individual behavioural level. First, population process can affect estimates of density and survival which may affect the interpretation of these metrics. Second, habitat properties, in particular foraging opportunities may cause missed opportunity cost to differ between habitats. In addition, individual state of a squirrel, in particular factors associated with fitness can affect GUD and also marginal value of energy, whereby in individuals which will obtain a greater increase in fitness for a given energy gain may have lower GUDs. Finally, individual state could interact with habitat to affect GUD, such that a high marginal value of energy in shrub-tundra could be caused by nearby high quality habitat and potential colonisation opportunities.

Population processes

Processes such as permanent emigration can affect the interpretation of population parameters as an indicator of habitat suitability. In my population models, temporary emigration was incorporated in to the estimation procedure so only permanent emigration is of concern when interpreting population parameters. Permanent emigration can reduce estimates of apparent survival, as individuals which have died cannot be differentiated from those which have emigrated (Lebreton et al. 1993). Permanent emigration can occur if habitat is poor suitability or as a result of density dependence in populations at high density. If emigration is a response to poor suitability habitat, incorporating this in to survival estimates represents a fair reflection of habitat suitability. However, if emigration is a response to high density in high suitability habitat this may cause lead to underrepresentation of suitability and value as a source population. In this study, it is more likely that density dependent processes in high suitability habitat would lead to an underestimate of suitability of tundra rather than be reflected in low survival in shrub-tundra.

Missed opportunity costs

Missed opportunity costs can vary between habitats according to alternative foraging options within that habitat. Missed opportunity costs are the cost of the alternate opportunities missed (e.g. foraging, mating, territory defence, predator sensitivity) as a result of engaging in a given activity (Olsson and Molokwu, 2007). Habitats with higher marginal values of time, where alternative foraging options to experimental feeding trays have higher value, should be expected to have high GUDs. The importance of missed opportunity cost when comparing GUDs between habitats has been highlighted (Olsson and Molokwu 2007). However, it is unlikely that the value of forage differs substantially between shrub and shrub-tundra as these are similar communities, with very similar forage species available, therefore this is unlikely to be the cause of such marked differences in GUD between these two habitats.

Individual state

The importance of state dependent behaviour in foraging has been highlighted in critiques of GUDs and predictions from marginal value theorem (Nonacs 2001). Certain states tend to cause individuals to have longer residence times than predicted by marginal value theorem or lower GUDs than may be expected. State has also been shown to affect GUD in Skuas feeding at penguin carcasses (Hahn et al. 2005) and when individuals are nearing the end of life, lower than expected GUDs are found (Wajnberg et al. 2006).

The equations underlying GUDs can be used to make specific predictions as to the effects of state (Fig. 4.1). In particular low fitness can result in low GUD as an individual with low fitness may experience lesser costs associated with a given predation risk. High marginal values of energy (defined as the rate of increase in fitness with energy consumed) also give rise to lower GUDs, as energy consumed becomes more valuable to an individual. Since survival is lower in shrub-tundra it might be that expected fitness may also be lower. This has the potential to reduce GUDs. Further, if individuals in shrub-tundra have a higher marginal value of energy this may reduce GUDs relative to shrub. In this case, GUD would be a poor indicator of habitat suitability in shrub tundra, as individual state may be driving GUD.

Trends in mass between habitats highlight one complication associated with state-based arguments to explain differences in GUD between shrub and shrub-tundra. If individuals in shrub-tundra have low fitness, it seems surprising that masses were some of the highest across all habitats. In this case, there is little reason to expect marginal value of energy to be high, especially compared to shrub, where masses were considerably lower. One possibility is that low fitness is determined by high predation risk in shrub-tundra rather than poor energetic state as measured by mass. Low expected fitness is also predicted to result in low GUDs and may drive differences between shrub and shrub-tundra (Brown 2004)

Surrounding habitats interacting with internal state

The landscape context in which habitats occur may also have implications for state and subsequent effects on GUD. One possibility is that marginal value of energy is high in shrub due to future opportunities associated with nearby tundra. Arctic ground squirrels are territorial; in arena trials, territorial contests within sexes are generally won by the heavier competitor (Watton and Keenlyside 1974). Being proximal to tundra, shrub-tundra individuals may have opportunities to monitor tundra territories and usurp poor quality individuals or take over vacant territories; their ability to do this may depend on their mass. This might give rise to a high marginal value of energy in shrub-tundra where individuals are adjacent to tundra compared to more distant shrub. Although shrub sites supported higher densities and survival than shrub-tundra sites, current dynamics in shrub-tundra may be dependent on the surrounding matrix of habitat. If this is the case, current suitability may be less relevant with future altered climate where alpine tundra may be become more restricted or absent in some areas.

Limitations and prospects

Although this study included populations in all three habitat types, due to the spatial configuration of habitats and other considerations (Chapter 1), replication in the shrub-tundra habitat was limited to a single population. To further understand this system tests of these theories across additional ecotones would be advantageous.

Conclusion

Differences in suitability between open alpine tundra and more shrubby habitats suggest encroachment of woody species may have negative impact on the survival and density of arctic ground squirrels. This could reduce their role in these locations as major agents of disturbance through biopedturbation and as important food items to mammalian and avian carnivores. Their metapopulation structure and habitat preference could influence the response of this species to changing climate. Using arctic ground squirrel populations, I have highlighted the utility of integrating population and individual based habitat suitability indices to identify the complexities surrounding habitat suitability. The use of behavioural indices alone to assess habitat suitability could be particularly misleading given the role of individual state and habitat specific opportunities in determining behaviour, but their inclusion may help identify complex processes that cannot be determined from survival and density alone.

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Table 4.1. Model selection for survival, temporary movements and capture probability parameterization of arctic ground squirrels using the robust design model. Support for models incorporating variation in survival between habitats, seasonal variation in temporary emigration and immigration and temporal variation capture probability are compared to less parameterised models.

Survival	Emig.	Immig.	Capture prob.	AICc	ΔAICc	AICc weight	No. of Param.	Deviance
habitat	season	Season	time	2472.38	0.00	0.81	12	2492.29
constant	season	season	time	2475.25	2.88	0.19	10	2499.30
habitat	season	season	constant	2486.90	14.53	0.00	8	2515.07
habitat	constant	season	time	2492.37	19.99	0.00	11	2514.35
habitat	season	constant	time	2494.02	21.64	0.00	11	2516.01
constant	constant	season	time	2494.56	22.19	0.00	9	2520.68
constant	season	constant	time	2497.02	24.64	0.00	9	2523.13
habitat	constant	constant	time	2502.38	30.00	0.00	10	2526.43
constant	constant	constant	time	2505.06	32.69	0.00	8	2533.23
habitat	constant	season	constant	2518.14	45.76	0.00	8	2546.30
habitat	season	constant	constant	2532.54	60.16	0.00	8	2560.71
habitat	constant	constant	constant	2554.95	82.57	0.00	6	2587.21

Table 4.2. Comparison of models where habitat affects different seasonal components of survival of arctic ground squirrels under the robust design model.

Model	AICc	ΔAICc	AICc Weights	Num. Par	Deviance
Active season only	2470.58	0.00	0.61	12	2490.49
General effect	2472.38	1.79	0.25	12	2492.29
Different effect	2474.18	3.60	0.10	14	2489.93
Overwinter only	2475.90	5.32	0.04	12	2495.81

Table 4.3. Summary of individual and population responses to habitat type in female adult arctic ground squirrels. In particular the similar individual measures recorded in shrub-tundra and tundra, despite very different responses at the population level.

	Population measures		Individual measures	
Habitat	Survival	Density	Adult mass	GUD
Shrub	Intermediate	Intermediate	Low	High
Shrub-tundra	Low	Low	High	Low
Tundra	High	High	High	Low

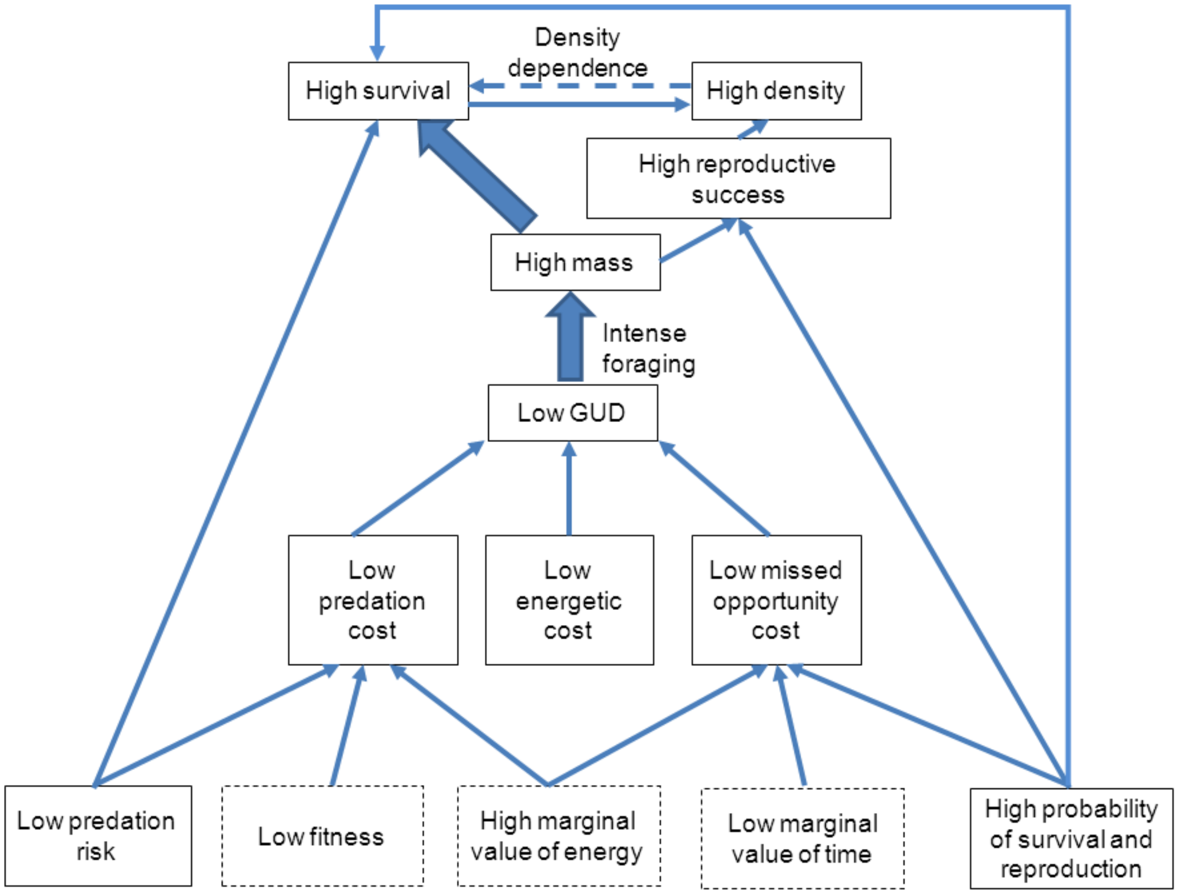

Figure 4.1. Relationship between components of giving up density (GUD) and population processes. Solid lines show links between states at individual and population levels. Dashed arrow indicates negative effects of high density on survival. Dashed boxes show individual and habitat states which may lead to differing predictions of suitability from behavioural and population indicators of habitat suitability.

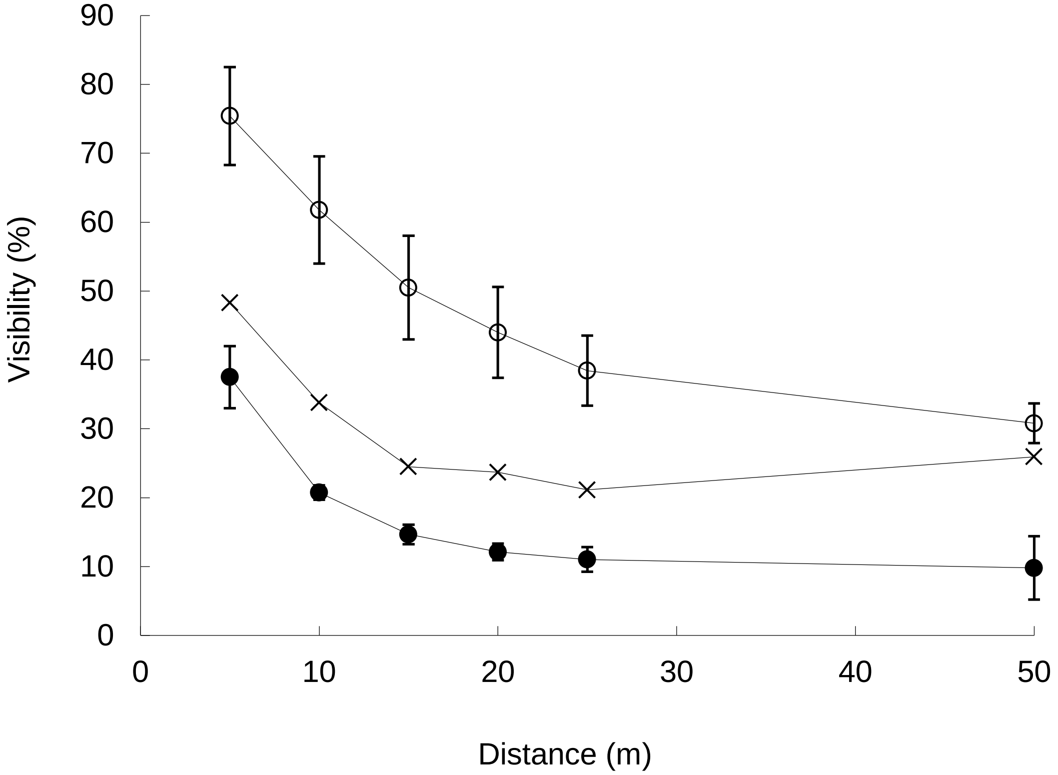

Figure 4.2. Visibility taken from 20cm above ground in all eight grids, shrub habitat (closed symbols), shrub-tundra (cross) and tundra (open symbols) are compared, 95% confidence limits between sites are shown for shrub and tundra.

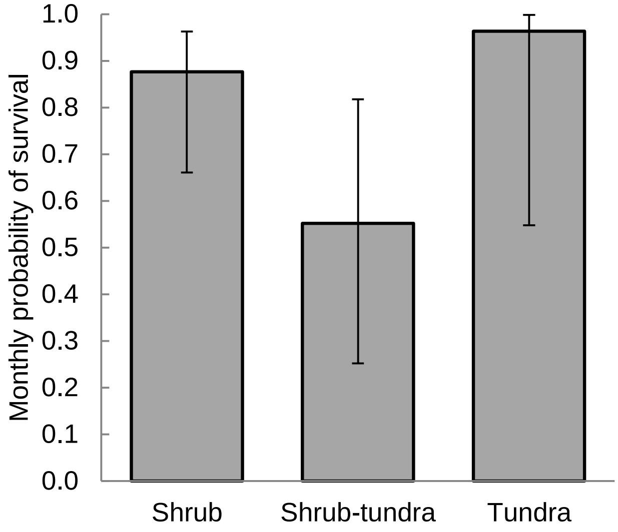

Figure 4.3. Best estimates of adult female active season survival under robust design (temporary movements) model. Values are survival estimate ± 95% confidence interval.

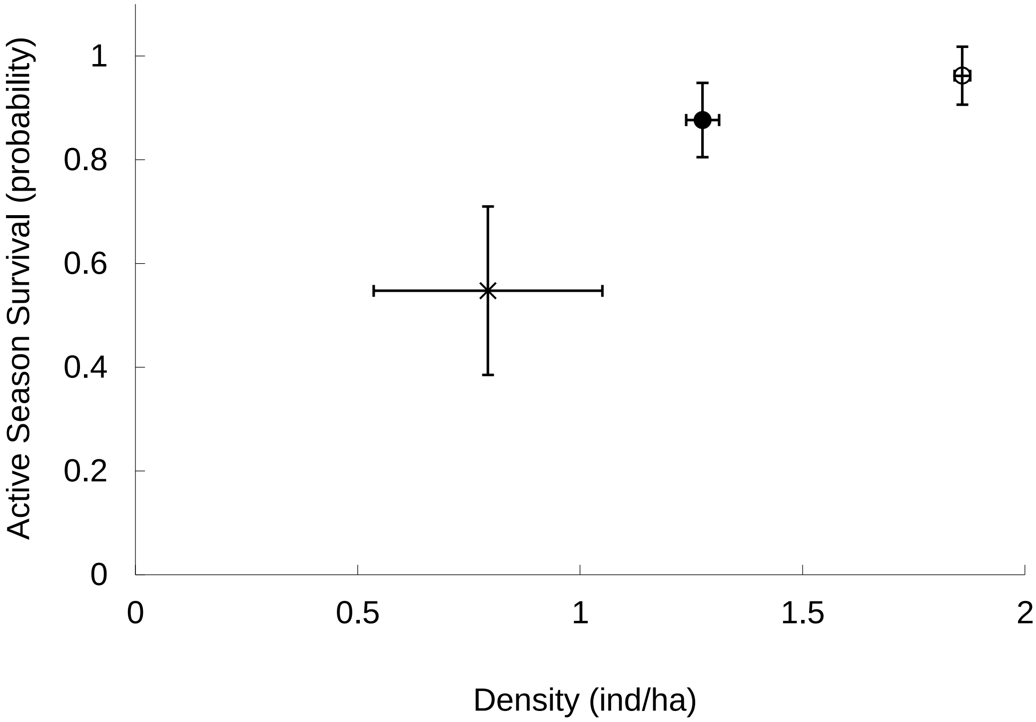

Figure 4.4. Association between July density and survival for adult female arctic ground squirrels in tundra (closed circles), shrub-tundra (crosses) and shrub (closed circles). Estimates reflect means across years when interannual variability in survival is assumed. Error bars indicate ±1 SE.

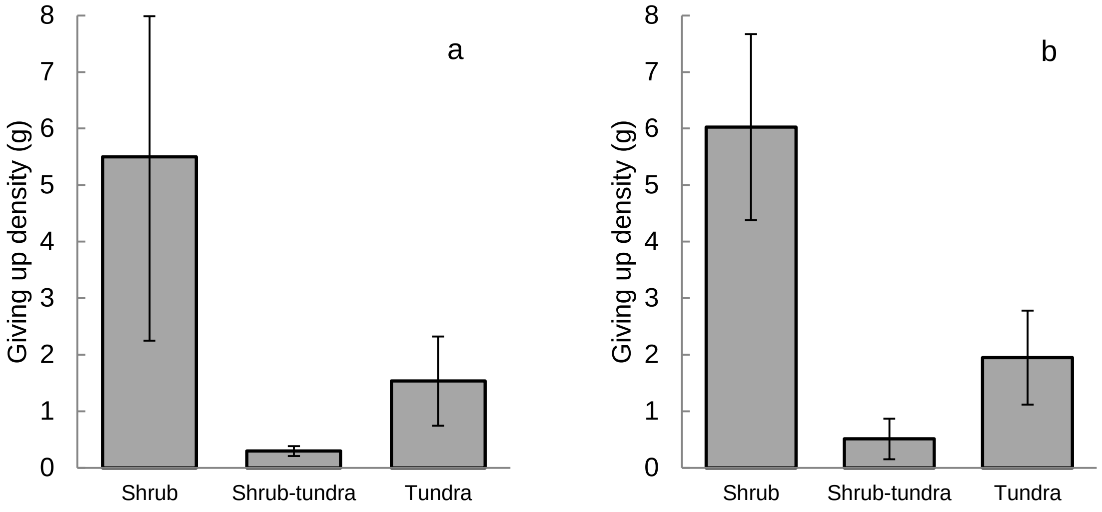

Figure 4.5. Giving-up density in habitats across and alpine tundra to shrub ecotone for a, adult females only and b, all demographic groups. Values are mean ± 95% confidence interval.

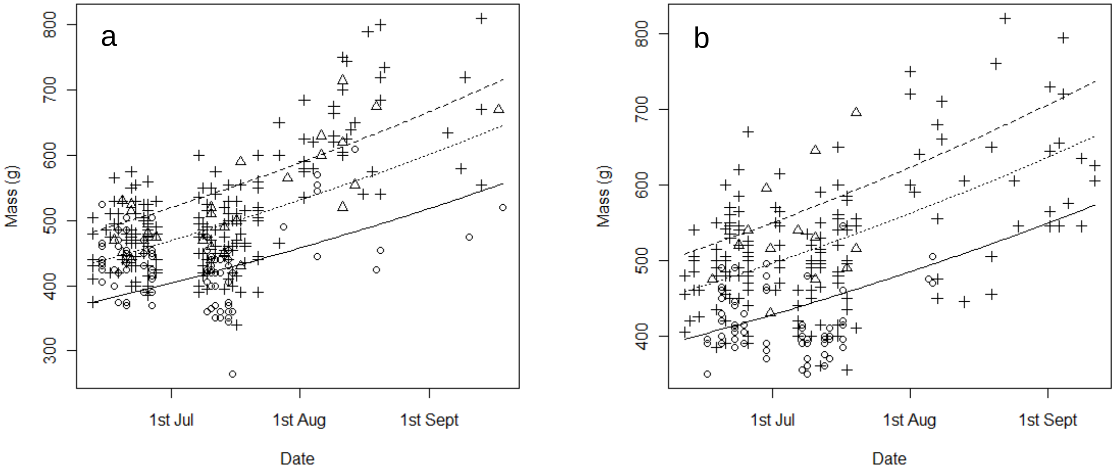

Figure 4.6. Trends in mass in a, 2008 and b, 2009 for adult female arctic ground squirrels and estimated relationships in tundra (+, dotted line), shrub-tundra (Δ, dashed line) and shrub (o, solid line).

Chapter 5

Reproductive investment and juvenile health in relation to shrub cover: Assessing the relative roles of density and habitat suitability

Introduction

Arctic ground squirrel habitats are currently in transition as a result of global warming (Chapter 2). As warming continues, habitat change has the potential to considerably affect the ecosystem role of arctic ground squirrels via changes in density and distribution (Chapter 3). The potential demographic and behavioural effects of these changes require an examination of reproductive effort and other influences on juvenile survival and growth among habitat types.

Woody, canopy forming species such as shrubs and trees are expanding their distribution (Danby and Hik 2007; Myers-Smith et al. 2011; Elmendorf et al. 2012). Encroachment of woody, canopy-forming species to more northerly latitudes and higher elevation, and local increases in density of these species are likely to reduce the area of arctic ground squirrel habitat that comprises open, high-visibility tundra. Increased incidence of taller canopy forming vegetation could have a number of effects upon habitat suitability for arctic ground squirrels.

Changes in visibility may alter the local predation regime and predation risk for arctic ground squirrels (Chapter 4). Non-consumptive effects of predators can be an important component of predator-prey dynamics (Peckarsky et al. 2008); potential indirect effects of predators on prey fecundity are not necessarily limited to those mediated through reduced net energy income, although this appears a major contributor

(Preisser and Bolnick 2008). Additional factors may include effects of predation risk upon conspicuous reproductive behaviours such a mate finding and mating. In arctic ground squirrels, mating occurs in burrows, this may reflect a behavioural mechanism to reduce predation risk.

Foraging responses to predation risk have the potential to affect maternal body condition, which is known to have an important effect on reproduction. In Richardson's ground squirrels, increased maternal body condition results in increased litter mass and increased neonate mass (Dobson and Michener 1995). In Columbian ground squirrels, mothers in better condition wean higher mass offspring which grow at faster rates (Skibiel et al. 2009). Columbian ground squirrels are an income-breeder, reproductive investment is affected by condition but depends perhaps to a greater extent on energy consumption (Broussard et al. 2003), which may also be affected by predation risk. In arctic ground squirrels, reproduction may increase with improved maternal condition and nutrition. Non-consumptive effects of predators, predator exclosure and food addition have caused increased body condition, lactation rates and higher percentages of litters to be weaned and as well as greater litter size (Karels et al. 2000).

Postpartum juvenile condition may also be affected directly by habitat suitability related to predation risk through more direct non-consumptive effects of predators on juveniles. In mammals, including sciurids, juvenile mortality is often higher than in later life stages (Sibly et al. 1997). Juveniles may be at particularly high risk of predation due to their size and inexperience. The need for high mass gain during this period may create a particularly intense trade-off between foraging and minimising predation risk (Arenz and Leger 2000).

Where habitats differ in suitability, density also often reflects suitability, with more suitable habitat supporting higher densities (Chapter 4). This can have effects on reproductive investment and early juvenile characteristics. Effects of density on reproductive investment and early juvenile characteristics may oppose those resulting from differences associated with trait-mediated responses to differences in predation risk between habitats. Density dependence in reproductive rates is common in ground squirrels (Oli et al. 2001). In arctic ground squirrels, both density dependent and density independent components govern reproduction (Karels and Boonstra 2000). To understand the likely effects of habitat suitability upon reproductive output and juvenile characteristics an understanding must be developed of the relative role of density independent effects of habitat suitability and density dependence associated with habitat-driven differences in density.

In this chapter I compared reproductive output between populations of arctic ground squirrels inhabiting tundra, shrub-tundra and shrub. I then assessed juvenile quality subsequent to emergence using measures of juvenile growth and parasite load. The relative effects of habitat suitability (from other population level processes, Chapter 4) and density upon these indices of reproductive investment and subsequent juvenile quality were investigated.

The effect of habitat suitability on reproductive output and juvenile condition is more dominant than density effects, consistent differences between shrub and tundra habitats were expected: tundra would be predicted to have higher reproductive output and better condition juveniles. Where density has dominant effects, reproductive output was expected to be greater and juvenile condition higher at low density sites. Lower habitat suitability appeared to result in reduced density (Chapter 4), and this correlation between suitability and density may result in lower suitability sites having greater reproductive output and juvenile growth where density effects predominate.

Methods

Trapping and population data

Eight populations of arctic ground squirrels in three different habitats were studied in an alpine valley in the Ruby Range, southwest Yukon, (61°21′ N, 138°27′ W). Capture-recapture trapping was conducted across 250m by 250m grids using Tomahawk traps (Tomahawk live trap llc, Hazelhurst, USA) at 50m spacing. Four grids were located in tundra, one in shrub-tundra and three in shrub. Each grid was trapped five times each month within a two week period toward the start of the month. Each trapping session lasted three hours with hourly checking of traps. Upon capture, squirrels were individually marked with Monel no. 1 tags (National Band and Tag Co, Newport, USA) and weighed, sex and reproductive status was ascertained including whether an individual was lactating. Zygomatic arch breadth was measured and faecal samples were taken where available for assessment of coccidial infection. Techniques were approved by the University of Alberta Animal Care Committee and followed the guidelines of the Canadian Council on Animal Care.

Condition indices for juveniles were derived at each trapping occasion for each trapped individual as residuals from a linear regression between zygomatic arch breadth and individual mass. Regressions were performed separately for each sex. Local population density was calculated each month from the five primary trapping occasions conducted at each grid.

Juvenile abundance and female reproductive output

Juvenile abundance in their natal habitat at each site in July was estimated using Huggins' estimator (1991). To assess reproductive output per female, this was divided by estimates of female population size in July, which were estimated separately using a modified version of the same estimator, whereby the first capture of each individual was excluded from estimates to remove the influence of transient individuals upon abundance estimates. This tends to inflate error associated with estimates but reduces bias as a result of occurrence of transients (Pradel et al. 1997). Abundance estimates for June for males and females were used to assess the effects of adult density on female reproductive output, as this represents the earliest available abundance for that year. Abundance estimation was implemented in the program MARK.

Differences in juvenile abundance and mean female reproductive output were tested for between years and between habitats using an ANOVA, which also incorporated a year effect. Shrub-tundra was necessarily excluded from this analysis given there was only one grid of this habitat type (however estimates are given in Table 5.5).

Juvenile growth and September mass

The effect of habitat suitability and local population density upon juvenile growth rates was assessed for the period July 1st to August 25th in 2008 where additional trapping effort was conducted throughout the summer to assess changes in mass. Coefficients from regressions of mass against dates, representing daily growth rate were compared between habitats. However, no juveniles were caught in shrub-tundra in 2008.

During this period, growth rates fit linear models well ($R^2>0.95$ in 82% of cases, minimum $R^2=0.82$) and therefore linear models were fitted throughout. In order to be included in the analysis, a minimum of four measurements of mass had to be made during this period, to ensure growth estimates were of sufficient accuracy. In addition one mass had to be taken prior to July 20th. Given juveniles emerge in early July in this area, disperse 2-3 weeks after emergence (Byrom and Krebs 1999) and are thought to settle in their new habitats by mid-August (Green 1977), the chosen criteria for these data should maximise the chances that growth rates represent those of individuals in their natal habitat. To assess the effect of habitat suitability and local habitat density upon mass prior to hibernation, the nearest possible mass to 5th September (± 3 days) was taken for each individual.

The effect of habitat type, local density (from adult July density) and sex upon growth rate and pre-hibernation mass were considered as well as interactive effects between habitat and local density. Models were compared using AICc. All statistical analyses were performed in R (version 2.13.0). After log-transformation, growth rates did not differ from normality at $\alpha=0.01$. Masses did not differ from normality at $\alpha=0.01$ so no transformation was applied. Given the lack of spatial replication within habitats, particularly in shrub-tundra an alternate approach to assess relationships between vibility and juvenile growth and mass. Analyses were performed to consider the effect of visibility experiences by individuals at multiple scales, local adult squirrel density, sex and year upon juvenile growth and juvenile mass (see Appendix)

Juvenile parasite load

Coccidial infection prevalence and intensity were estimated from counts of coccidia in faecal samples from trapped juvenile female arctic ground squirrels. Faecal samples were taken in July, August and Sept in 2008 and 2009. Directly after collection, 1g faeces was placed in 5ml 2% (w/v) potassium dichromate solution and stored at ambient temperature in the field until late September, after which they were refrigerated at 4°C. Samples were processed by three technicians using a blind protocol. Counts of faecal coccidian oocysts were made from centrifugal faecal floatations with Sheather's solution. Calibrations between technicians were applied and returned R^2 values of 0.99 and 0.64, the latter representing a subset of data only representing lower parasite counts, and correction factors were applied to adjust for differences between technicians.

Relative support for effects of habitat, local population size, individual condition and month and year on both parasite prevalence and intensity were considered using model selection and model weights with small sample-corrected Akaike's Information Criterion (AICc). Effect of these factors upon parasite prevalence was analysed using a generalised linear mixed model with binomial error structure, with squirrel identity and a random effect. Given infection prevalence was 100% in 2009, these trends were only assessed for 2008. Trends in parasite intensity in infected squirrels were assessed using a linear mixed model with a random squirrel effect. After log transformation, distribution of parasite infection intensity did not differ from normality and α=0.05.

Results

Juvenile abundance and female reproductive output

Substantial variation in juvenile density was observed within habitats (Fig. 5.1). Between habitats there was no evidence for consistent differences in juvenile abundance ($F_{1,11}$=2.57, p=0.14, Fig. 5.1a, Table 5.5). Density dependent effects on juvenile abundance were not identified ($F_{1,11}$=1.93, p=0.19). Much greater variability was seen between juvenile production in tundra (4-27 individuals within 4ha sites), than production in shrub, which was consistently low (2-10 individuals).

There were no consistent effects of habitat type or density upon reproductive output ($F_{1,11}$=0.10, p=0.7 and $F_{1,11}$=0.94, p=0.4, respectively, Fig. 5.1b). However, tundra sites were generally at higher density than shrub sites, so power to discern differences was probably low. There appeared to be relatively little interannual variation in reproductive output within sites, suggesting other components of suitability unrelated to the extent of shrub may affect interpretation of this data (Fig. 5.2).

Juvenile growth and September mass

Juvenile growth rates in 2008 were lower in shrub than in tundra (w_+=0.90, Fig. 5.3, Table 5.1, Table 5.5) and were higher for males than females (w+=1.00) but did not show any trend associated with local density (w_+=0.23). Predictions from juvenile growth rate relationships between shrub and tundra appear to suggest that juvenile masses are likely to be most similar in early to mid-July, suggesting mass at emergence is relatively similar between habitats and diverges subsequent to this (Fig. 5.4). In 2009, less data were available for testing, however mean growth rate for male and female juveniles in shrub-tundra appeared similar to those in tundra (Table 5.5).

Individuals in tundra had higher mass in early September than individuals in shrub with individuals in tundra being on average 104g heavier than those in shrub (w_+=0.96, Table 5.2). Males were on average 45g heavier than females (w_+=0.66). Inverse density dependent effects on mass were observed (effect size=-0.7±0.3g $\text{ind}^{-1}\ \text{ha}^{-1}$, w_+=0.69).

Juvenile parasite load

Juvenile coccidial infection was generally high, with 88% of faecal samples collected having coccidial parasites present. Increased probability of infection was associated with high local density of squirrels (w_+=0.725, Table 5.3, Fig. 5.5). Prevalence of infection was greater in 2009, where all individuals were infected, than in 2008, which was associated with an 82.9% infection rate. Habitat appeared to have little effect on coccidial prevalence other than that imposed by local density. For those individuals infected, there appeared to be considerable temporal effects upon infection intensity, with greater parasite loads in 2009 than 2008 (w_+=0.726) and with monthly variation in infection intensity (w_+=0.747, Table 5.4, Table 5.5). Local population density and habitat had no effect on infection intensity.

Discussion

I found reproductive output to show relatively little direct association with habitat type or local density, but observed juvenile growth rates to be higher in apparently high suitability tundra habitats. Dense shrub supported lower growth rates than tundra and was associated with lower pre-hibernation masses than tundra. Variation in parasite prevalence in juveniles was associated with density but did not show strong habitat associations. In addition to the identified effects of habitat and density, further underlying effects may be less apparent than expected in some cases due to variation in site suitability for juveniles associated with local hydrology, and temporal trends associated with weather rather than broad habitat classifications.

Juvenile abundance and female reproductive output

No clear linear effects of density or habitat appeared to explain variation in the number of juveniles produced at a site or female reproductive output, however there is probably still some role of density and habitat in determining levels of reproduction, albeit combined with more local effects relating to hydrology, predation risk and other environmental factors. Tundra contained some of the sites producing the greatest number of juveniles for a given population compared to shrub-tundra and shrub, however tundra also contained some habitats with quite low densities of juveniles. This spatial variation may reflect differing drainage, extent of soil development and local effects of predators (Chapter 2). For example, one tundra habitat was particularly prone to flooding during July and dead altricial young were observed apparently flushed out of this site after a heavy rainfall event in 2009; this site had some of the lowest number of juveniles produced of all tundra sites (Tundra 4, Fig. 5.2). Although many of the tundra sites had the greatest number of juveniles in July, these appeared to reflect a larger number of reproductive females rather than increased female reproductive output.

Although there were no significant differences in juvenile production at the population level or in terms of reproductive output between habitats, tundra appeared to have a much higher absolute production of juveniles relative to other habitats in its most productive sites, but not a higher individual reproductive output. This may suggest some role of density dependence in determining reproductive investment. The lack of relationship between local population density and reproductive output suggests that if present, this relationship is complex and also involves additional factors untested in this study. In Columbian ground squirrels older female ground squirrels are known to show senescence (Broussard et al. 2003). This may reduce mean reproductive output in habitats where individuals have higher survival. Individual based data on age and reproductive output would help determine whether this was a contributing factor to reproductive output in arctic ground squirrels. In addition, reproductive investment of an individual in one year may affect that in the subsequent year, with the cost of reproduction the previous year reducing resources the next (Huber et al. 1999). In many sites, reproductive output appeared to vary considerably between years, this may reflect potential lagged effects of the previous year’s reproductive effort.

Juvenile growth and September mass

Juvenile growth was habitat and sex dependent. Juvenile growth showed similar trends to those seen in adult female mass (Chapter 4), with juveniles in shrub exhibiting slower growth rates than those in tundra or shrub tundra. Growth rates were very similar to those previously reported in a more northerly population (7g/day for males and 5g/day for females, Buck and Barnes 1999). Lower juvenile growth rates in shrub, may reflect increased predation risk for this species. Individuals in shrub appear to be more wary foragers, in particular appearing to move more frequently between foraging patches. Increased predator-sensitive foraging may in part explain variation in growth rate between shrub and other habitats (Chapter 6). In addition to reducing predator detection distances, shrub has been shown to decrease ability to escape predators for juvenile ground squirrels of other species via creating obstructions in escape pathways, this may lead to an increased need for predator sensitivity and greater associated energetic costs (Schooley et al. 1996).

Assuming a linear mass increase from parturition to mid-August, variation between habitats in terms of juvenile growth seemed to be reflected in differences in mass gain subsequent to emergence. Masses appeared more convergent earlier in the season. This either suggests that female provisioning for offspring and parturition date are similar across habitats, or that both parturition and provisioning differ between habitats in a manner that results in similar mass upon emergence. This would require adult females to compensate for late parturition with greater provisioning prior to emergence.

In other species of ground squirrel, both condition and energy consumption can effect reproductive investment (Broussard et al. 2003), so this remains a possibility.

Variation in growth rates between habitats could have important long-term implications for subsequent survival in different habitats. Ground squirrels may delay dispersal until they reach a threshold mass (Green 1977; Nunes and Holekamp 1996). Dispersing later and having lower mass at dispersal may reduce ability of individuals to compete for high suitability habitats, and ultimately reduce their lifetime reproductive success and individual contribution to population growth. As such, these initial differences in growth between habitats have the potential to have effects extending far beyond dispersal from the natal habitat. This could greatly reduce the contribution of shrub habitats to growth at the metapopulation level.

Juvenile parasite load

Coccidial infection did not appear to be substantially affected by habitat, but did show considerable temporal variation and was influenced by local density. In general, greater parasite prevalence and intensity was observed in 2009 compared to 2008. Whether this represents a stochastic event related to a heavy outbreak in 2009 or a response to underlying environmental conditions is unclear. Increased density also caused an increase in parasite prevalence, most likely as a result of increased transmission rates. It therefore appears that density rather than habitat suitability has stronger effects on transmission rates. When considering potential negative effects of coccidia upon arctic ground squirrels, the extent of infection is likely more important than occurrence for animal health. Although coccidial infection has appeared quite benign in some cases

(Seville et al. 1992), in other cases it has been associated with morbidity for ground squirrels (Todd Jr. et al. 1968). In high density areas, individuals susceptible to intense infection may have greater chance of initial infection due to increased transmission rates, however infected individuals in these dense habitats do not seem to have higher parasite loads. This may be a result of antagonistic effects of density and suitability within habitats upon condition

Conclusions

Of all indicators of juvenile production and quality, juvenile growth was most strongly related to habitat. Individuals had higher growth rates in tundra than in shrub. Given shrub habitats are associated with a higher costs of foraging and associated with adult female mass (Chapter 4), these lower growth rates may be associated with increased predator-sensitive foraging and lower foraging efficiency or possibly lower maternal investment from poorer condition mothers. Given that juvenile masses appear to diverge most subsequent to weaning, it seems more likely that these differences in growth are habitat driven.

In terms of reproductive output and parasite load, there were no substantial differences between habitats. Trends in reproductive output were probably driven by a number of factors which may include habitat and density (although this was not determined in this study), but also may to include risk of burrow flooding associated with topography and aspect, local variation in predator use and delayed effects of reproductive costs in the previous year. Parasite load appears to be affected by local squirrel density, but only in terms of transmission rates as suggested by the fact that parasite prevalence increases with local population density but infection intensity appears to be relatively independent of habitat and density. This may be because the coccidian parasite *Eimeria*, is relatively benign in this species and infection levels reflect stochastic processes.

In general, the potential for antagonistic effects between habitat and density may reduce differences in reproductive investment of adults and condition of juveniles subsequent to weaning between habitats. However, I did find that despite the potential for increased competition under increased densities, juvenile arctic ground squirrel exhibited lower initial growth rates subsequent to emergence in shrub than tundra. This may be driven by differences in habitat suitability between these two habitats.

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Table 5.1. Model selection of factors affecting juvenile growth rates in 2008 in shrub and tundra habitats. Effects of habitat, sex, local density, and a habitat by local density interaction are included in the model set. Best six models are shown in addition to a null model.

Model	AICc	∆AICc	No. parameters	Model weight
Habitat, sex	-13.84	0.00	4	0.69
Habitat, sex, local density	-11.07	2.54	5	0.17
Sex	-9.35	4.49	3	0.07
Habitat, sex, local density, habitat*local density	-7.61	5.81	6	0.03
Sex, local density	-7.17	6.55	4	0.02
Habitat	-2.26	11.58	3	0.00
Null	0.05	13.89	2	0.00

Table 5.2. Model selection of factors affecting juvenile September mass in 2008 in shrub and tundra habitats. Effects of habitat, sex, local density, and a habitat by local density interaction are included in the model set. Best six models are shown in addition to a null model.

Model	AICc	∆AICc	No. parameters	Model weight
Habitat, sex, local density	208.65	0.00	5	0.41
Habitat, local density	210.16	1.51	4	0.19
Habitat, sex	210.21	1.56	4	0.19
Habitat	211.65	3.00	3	0.09
Habitat, sex, local density, habitat*local density	212.93	4.28	6	0.05
Habitat, local density, habitat*local density	213.48	4.83	5	0.04
Null	215.55	6.90	2	0.01

Table 5.3. Model selection of factors affecting parasite prevalence in juvenile female arctic ground squirrels. Effects of habitat, year, month, local density and individual condition are considered. Best five models are shown in addition to a null model.

Model	AICc	ΔAICc	No. parameters	Model weight
Year, local density	79.31	0.00	4	0.30
Year, month, local density	80.35	1.04	6	0.18
Year, local density, individual condition	81.31	2.00	5	0.11
Year, month, local density, individual condition	82.29	2.98	7	0.07
Year, month	82.50	3.19	5	0.06
Null	89.03	9.72	2	0.00

Table 5.4. Model selection of factors affecting parasite infection intensity in juvenile female arctic ground squirrels infected with coccidia. Effects of habitat, year, month, local density and individual condition are considered. Best five models are shown in addition to a null model.

Model	AICc	ΔAICc	No. parameters	Model weight
Month, year	436.36	0.00	5	0.43
Habitat, month, year	438.58	2.21	6	0.14
Year	438.59	2.22	3	0.14
Month	438.69	2.33	4	0.13
Habitat, month	440.39	4.03	4	0.06
Null	442.56	6.19	2	0.02

Table 5.5. Summary of variation in Indicators of investment in juveniles and subsequent juvenile health in tundra, shrub-tundra and shrub habitats for arctic ground squirrels. Predicted direct effects of habitat suitability and predicted effects of habitat suitability mediated through density are given.

	Year	Predicted effect of habitat suitability	Predicted effect of density	Shrub	Shrub-tundra	Tundra	Other factors (factor level where higher)
Juvenile production (individuals)	2008	Tundra > Shrub > Shrub-tundra	Shrub > Shrub-tundra > Tundra	2.43±0.70	0	2.82±2.27	
	2009			1.11±0.50	1.65	3.07±1.17	
Reproductive output (juveniles female $^{-1}$)	2008	Tundra > Shrub > Shrub-tundra	Shrub > Shrub-tundra > Tundra	3.01±1.57	0	1.48±0.45	
	2009			2.57±1.72	6.00	2.59±1.80	
Juvenile growth rate (g day^{-1})	2008	Tundra > Shrub > Shrub-tundra	Shrub > Shrub-tundra > Tundra	F: 4.77±0.08^{a} M:6.74±0.20^{b}	NA	F: 6.11±0.28^{a} M:7.91±0.60^{b}	Sex (Male)
	2009			NA	F: 5.61±0.17 M:6.68	F: 5.52±0.28 M: 7.16±1.12	
September mass (g)	2008	Tundra > Shrub > Shrub-tundra	Shrub > Shrub-tundra > Tundra	F: 431.67±10.14 M:590	NA	F: 523.75±32.35 M:630.83±36.09	
Infection prevalence (% infected)	2008	Shrub > Shrub-tundra > Tundra	Tundra > Shrub > Shrub-tundra	75.0%	83.3%	87.5%	Local density (High) Year (2009)
	2009			100.0%	100.0%	100.0%	
Infection intensity log$_{10}$(oocyst frequency)	2008	Shrub > Shrub-tundra > Tundra	Tundra > Shrub > Shrub-tundra	4.95±0.52	4.71±1.16	4.84±0.30	Year (2009)
	2009			7.71±1.08	5.05±0.61	5.97±0.43	Month

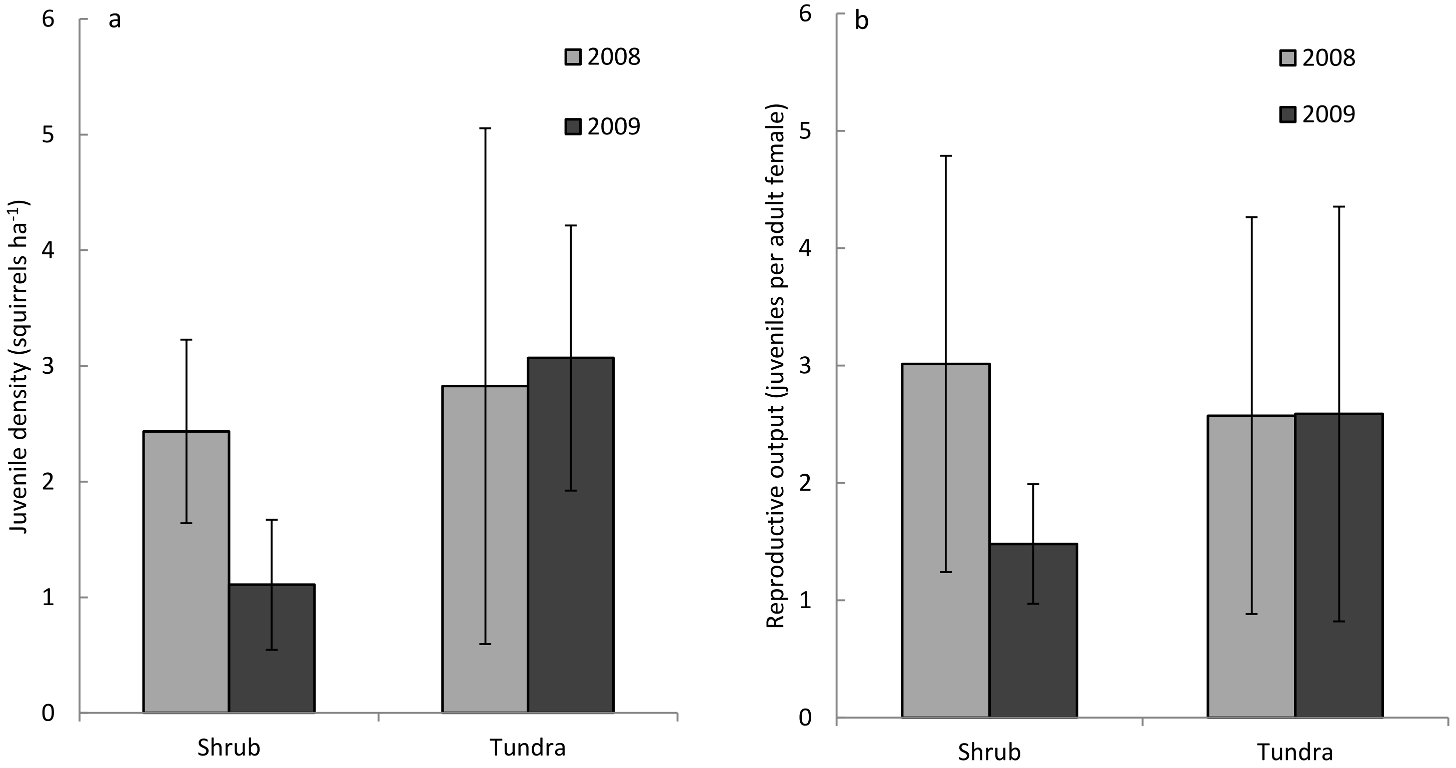

Figure 5.1. Variation in investment in juveniles between habitats a) at the population level showing number of juveniles in July within four-hectare sites, b) for each female showing variation in mean reproductive output. Values are mean ± 95% confidence interval.

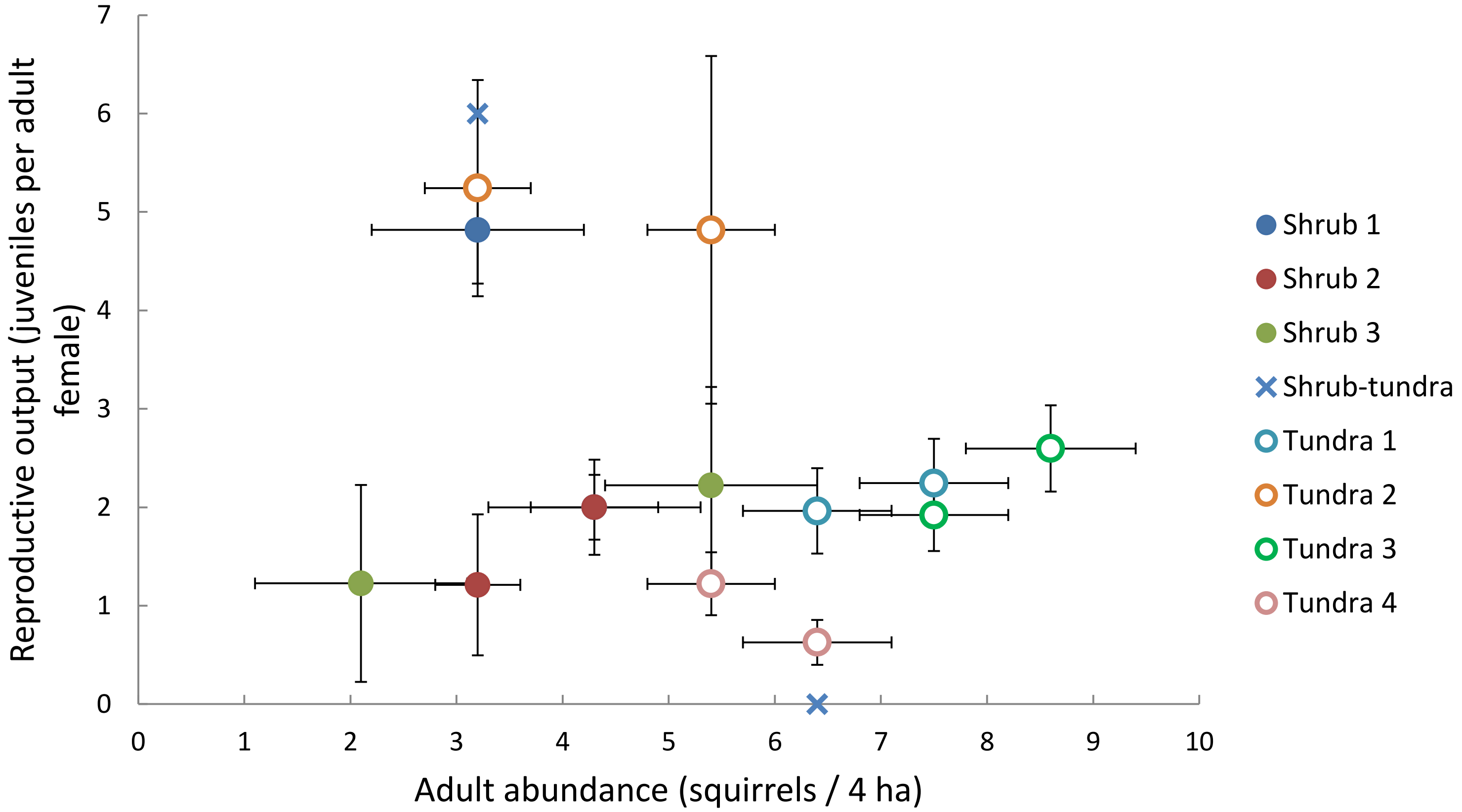

Figure 5.2. Correlation between adult abundance and reproductive output in shrub (closed circles), shrub-tundra (crosses) and tundra (open circles). Temporal replicates of each site (census conducted in 2008 and 2009) in each habitat are shown. Estimations are ± 1 S.E.

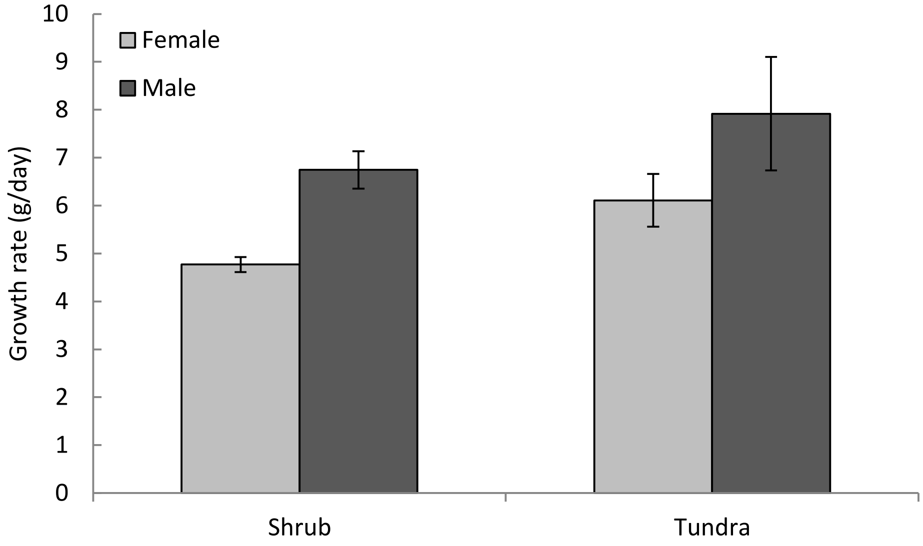

Figure 5.3. Comparison of juvenile growth between shrub and tundra habitats in 2008. Differences between males and females are shown. Values are mean ± 95% confidence interval.

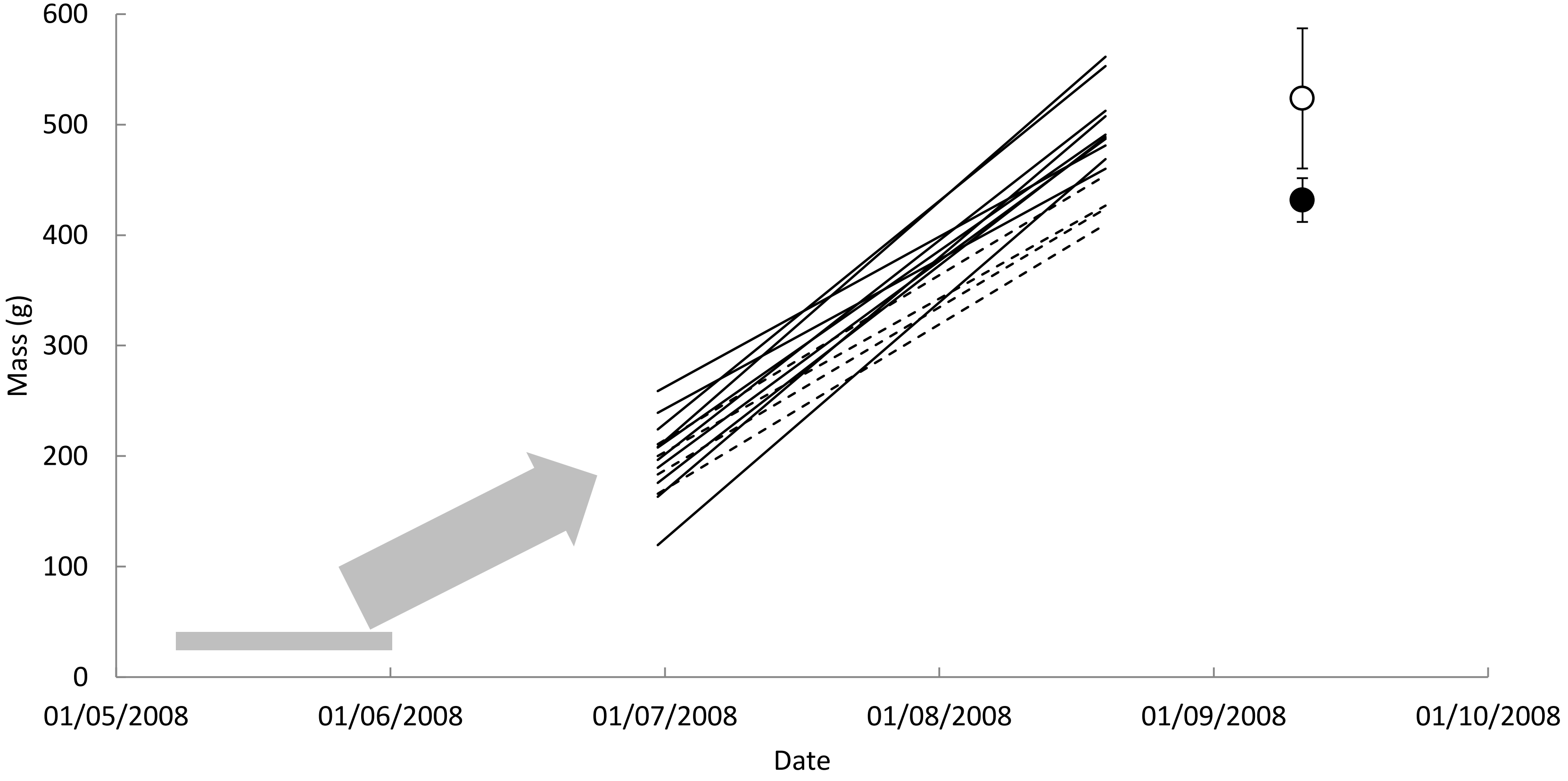

Figure 5.4. Predicted growth from regressions in shrub (broken lines) and tundra (solid lines) in 2008. It can be seen that in late June when juveniles emerge from burrows masses are similar, but diverge subsequent to this. September masses are shown for tundra (open circle) and shrub (closed circle) ± 95% confidence intervals. Grey area show approximate birth mass and arrow shows subsequent growth.

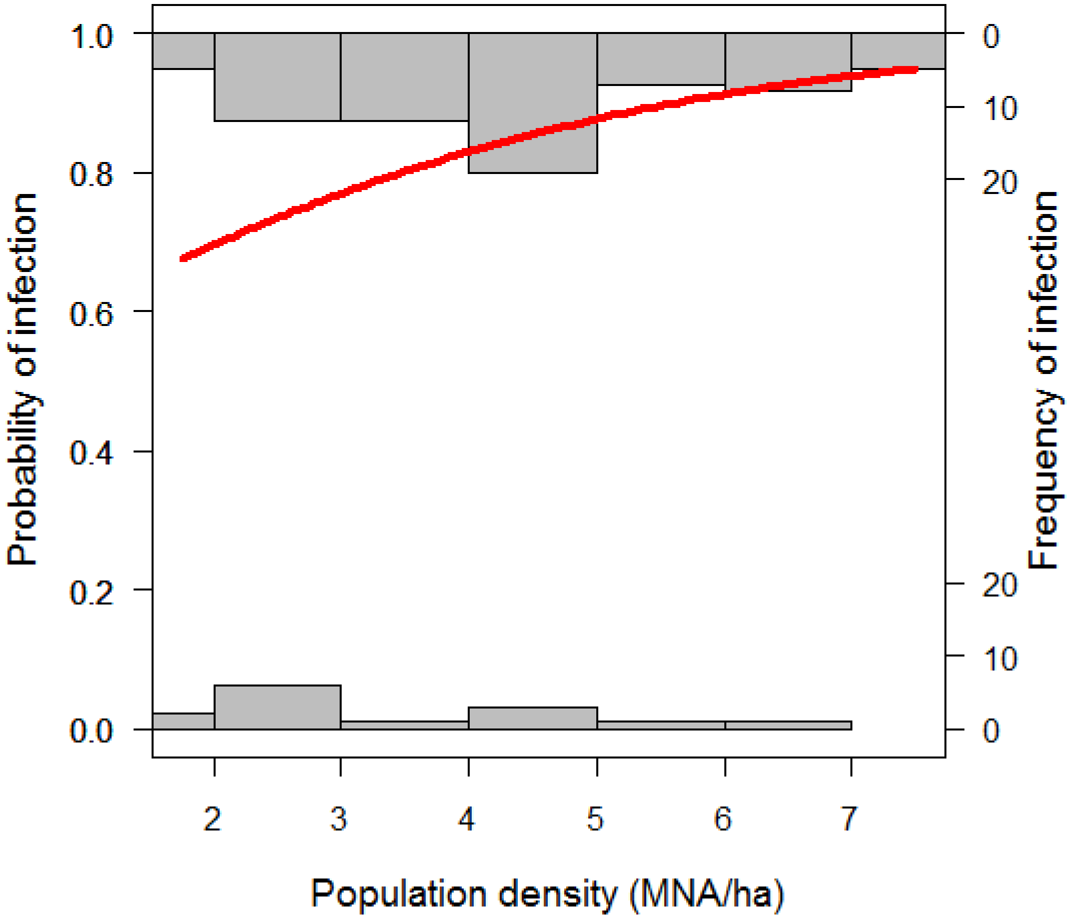

Figure 5.5. Effect of local population density upon probability of parasite infection in juvenile female arctic ground squirrels. Line shows probability of infection. Bars show frequency of uninfected individuals (bottom of graph) and infected individuals (top of graph).

Chapter 6

Giving up density, vigilance and alternate strategies to minimise predation risk across a shrub to alpine tundra ecotone: Assessing the implications of shrub encroachment for foraging costs for arctic ground squirrels

Introduction

Risk of predation has consequences at the population level, not only via direct effects of predator induced mortality, but also as a result of predator related changes in behaviour (Sinclair and Arcese 1995; Hik 1995). Trade-offs exist between avoiding predation and obtaining food. These decisions can be considered in a spatially hierarchical manner (Stephens 2008) and include choice of foraging location, first at the habitat then at the patch scale, as well as finer scale foraging decisions within a given location. Decisions often concern the allocation of time and energy to maximise fitness and include patch residency (Brown 1988), time allocation to vigilance and allocation of energy to predator-sensitive behaviours (Brown 1988; Lima and Dill 1990). By considering these different behavioural responses in concert, it is possible to achieve a fuller understanding of responses to predation risk.

Arctic ground squirrels inhabit a wide range of habitat types, and habitat shifts could reduce habitat suitability for this species. As climate shifts associated with global warming continue, boreal forest species and shrub vegetation are encroaching northward and to higher altitudes, expanding in to open arctic and alpine tundra (Danby and Hik 2007; Gottfried et al. 2012; Myers-Smith et al. 2011). This will have profound effects on habitat structure, reducing visibility where these taller, canopy forming species extend their distribution and increase their density.

Visual obstruction can have major effects on foraging behaviour (Embar et al. 2011). Predation risk is thought to be strongly associated with habitat visibility in arctic ground squirrels. In the boreal forest, exclosure experiments have demonstrated the role of predators in limiting abundance (Byrom et al. 2000), while at a more local scale, visibility seems to affect burrow site selection (Karels and Boonstra 1999). Although differences in population dynamics and stress levels between boreal forest and alpine tundra population are thought to be a result of differing predation risk (Gillis et al. 2005; Hik et al. 2001), direct evidence of either differences in predator induced mortality or predator sensitive behaviour between habitats have been lacking.

The harvest rate at which an individual leaves a foraging patch should reflect the optimal time to leave a patch to maximise fitness, in effect, the point at which the net energy acquisition rate ceases to increase over time (Charnov 1976). These ideas have been most commonly applied to models which incorporate benefits of intake rate and costs of travel time to assess net energy acquistition. Giving-up densities (GUDs, Brown 1988) develop this concept to reflect this same point where net fitness gain with food consumed ceases to increase, and takes account of multiple energetic, predation and missed opportunity costs of foraging when determining net fitness. I used this indicator to assess costs of foraging at the habitat and patch scale with particular reference to visibility and predation risk.

Beyond patch residency, many finer scale behavioural decisions may be used to maximise fitness while foraging under predation risk. These may also determine time and energetic costs associated with foraging. Increased investment in vigilance during foraging has been detected in response to increased predation risk where there is reduced visibility in alpine specialists (Ferrari et al. 2009), but may be complicated by the potential for obstructions to provide benefits as cover from attack and detection by predators (Hannon et al. 2006). Time allocated to vigilance diverts time and energy from foraging and therefore reduces foraging efficiency. This has the potential to increase foraging costs and reduce energy gain during foraging. In addition, these decisions may feedback to patch residency as they depress net rates of energy intake.

I evaluated the extent of predator sensitive foraging at multiple scales across three arctic ground squirrel habitats varying in visibility. Using behavioural observations from squirrels across an alpine ecotone, from dense shrub to transitional shrub-tundra and alpine tundra I first assessed the effect of visibility upon GUD at the habitat level. I hypothesised that more visually closed habitats have higher GUDs as individuals quit patches earlier due to high costs of predation risk.

I then assessed how local patch scale visibility affects GUD and whether the habitat context in which patches occur affects behaviour. I predicted that individuals in high visibility alpine tundra will have higher GUDs where visibility is low, due to an increased predation risk in these areas. In contrast I predicted that in more visually obscured habitats, high visibility patches may pose a greater risk, as individuals will have poor ability to detect predators, because of visual obstruction at the habitat scale but will be exposed to detection by avian predators and those which have better line of sight in such habitats due to their greater size.

Finally, I assessed whether foraging efficiency differs between habitats by examining the relationship between giving up density and time spent foraging and quantified the extent of vigilance in different habitats. I used these metrics to determine the most important effects of habitat and local visibility upon predator sensitive foraging.

Methods

Giving-up density

GUD was estimated for individual squirrels foraging in tundra, shrub-tundra and shrub habitats between late June and mid-August in 2009 and 2010. Trays where filled with 8g of quartered peanuts mixed randomly through 4l of clean sand. A single quartered peanut with peanut butter was placed exposed in the centre of the filled tray as an initial lure. Trays were monitored with two video cameras (IR bullet camera, 420 TVL and 4 channel DVR, Zurich Lock and Key, Illinois, USA). Footage was transmitted to a remote observer who monitored activity while obscured from line of sight of the tray at a distance of at least 300m (Spytronic, Quebec City, Canada). Squirrels were individually identified from unique dorsal alpha numeric painted using black hair dye. Individual markings allowed age, sex, mass and zygomatic arch breadth from trapping data (Chapter 4) to be attributed to each squirrel. Condition indices based on residuals from relationships between zygomatic arch breadth and mass for juvenile and adult, males and females were also calculated for each squirrel.

A GUD trial for an individual was deemed to have terminated when the individual left the tray for more than five minutes. The remaining peanuts were then weighed to determine GUD. If an individual only took the lure peanut the GUD was considered incomplete and excluded from analysis. If a squirrel was joined by another individual during foraging, the trial was also excluded. Individuals for which GUD had already been measured were also excluded from analysis if they returned on subsequent GUD trials to exclude potential effects of habituation to the GUD setup or increases in foraging effieciency associated with experience with this experimental design.

Local visibility

Line of sight was estimated at each GUD trial location. Percentage of a 1m by 1m board visible at a 10m distance was estimated across each of 4 cardinal directions. All observations were made from an eye-line of 20cm above ground.

Behavioural observations

From video footage, the time spent at the trial was assessed and the occurrence of vigilance behaviour was recorded. Video footage was reviewed at one quarter speed and behavioural events were recorded using an event recorder (JWatcher Video, version 1.5.0). Any incidence of the head being elevated above the back (either in quadrupedal or bipedal postures) was considered vigilance. Bipedal postures where individuals had a straight back were considered high cost vigilance. From this data, a time series of vigilance with respect to time on the GUD apparatus was developed.

Statistical analyses

Difference in GUD, total time at a trial, time vigilant and proportion of time vigilant between habitats were assessed using an ANOVA and Tukey *post hoc* tests. An arcsine-square root transformation was performed on proportion of time vigilant data.

Tests for relationships between time of day and GUD yielded no significant results at $\alpha=0.1$, therefore time of day was excluded from subsequent models. The relative effects of habitat, local visibility, the interactive effects of habitat and local visibility, individual condition index, age and the date the trial was conducted were assessed using model selection under AICc. As there were no *a priori* reasons to assume certain factors were likely to act in concert, all possible combinations of factors were included in the set of linear models in addition to a null model. Sum of weights (w_+) were used of assess the extent to which different factors were supported by the data.

The amount of time spent at GUD trays was compared between habitats using an ANOVA. Factors affecting the amount of time required to achieve a certain GUD were then assessed. The effect of habitat, visibility, habitat by visibility interactions, individual condition, sex, age and date of trial were all evaluated as factors affecting the relationship between GUD and time spent at a trial. AICc was also compared to a null model to ensure GUD was supported as an explanatory variable. Time spent at a GUD tray was log transformed to reflect an expectation of diminishing returns with decreasing GUD after which its distribution did not differ significantly from normality at $\alpha=0.1$. Analogous analyses were performed for the relationship between GUD and time spent foraging and time spent vigilant.

Temporal trends in the extent of vigilance in adults were assessed using a linear mixed model with individual as a random factor to assess the effect of time at GUD tray, habitat and interactions between time and habitat upon the proportion of time spent vigilant within 30 second intervals. Temporal autocorrelation was incorporated in to the model using a first order autoregressive model after testing for higher levels of autocorrelation. Data were truncated at 300 s because few squirrels in shrub habitat remained at GUDs past this time. A square root transformation of the proportion of time spent vigilant provided good fit to a normal distribution, further arcsine transformation resulted in significant departure from normality, so was omitted.

Effects of habitat and time spent at a GUD were evaluated with respect to the proportion of time spent undertaking high cost vigilance. The response variable was transformed using an arcsine cube root function as there was poor conformation to normality under an arcsine transformation. All analyses were performed in program R (version 2.13.0). All response variables did not show significant departure from normality at α=0.1.

Results

Effects of habitat upon GUD

GUD differed between habitats with shrub having considerably higher GUD than shrub-tundra or tundra ($F_{2,19}$=18.25,p<0.0001 and p<0.0002 in both Tukey post-hoc pairwise tests, Fig. 6.1a). Shrub-tundra and tundra both had low GUDs, GUDs in shrub-tundra were slightly lower although there was no significant difference in pairwise tests (p=0.38).

Habitat and local visibility both had substantial effect on GUD (w_+=1.00 and w_+=0.89. respectively, Table 6.1). The effect of visibility upon GUD differed markedly between habitats. GUD strongly declined as visibility increased in tundra, but increased very weakly with increased visibility in shrub-tundra (Table 6.2). A greater increase in visibility with GUD was seen in shrub (w_+=0.82 for habitat by visibility interaction, Fig. 6.2) however, only one shrub individual foraged in very low visibility, and so had potentially high impact on the final trend. As the relationship observed in shrub was highly dependent on a single individual which had a low GUD in a particularly low visibility patch (Fig. 2), model selection was run again with a reduced model set (containing only habitat, visibility and an interaction of the two) without shrub individuals. Strong support for differing responses to visibility between tundra and shrub-tundra were evident (ΔAICc=11.5 between habitat by visibility interactive model and next best model with habitat and visibility, this represented stronger support between these two models than when shrub was included ΔAICc=5.32). Different responses were therefore evident between shrub-tundra and tundra and also between tundra and shrub albeit with the caveat of low sample size. There was relatively little support for a strong effect of age, sex, condition or date upon GUD (w_+=0.10, w_+=0.21, w_+=0.20 and w_+=0.07, respectively).

Time allocation variation between GUDs

Despite relatively strong differences in GUD between habitats, there were no strong associations between the time spent foraging at a GUD trial and habitat ($F_{2,19}$=2.02, p=0.16, Fig. 6.1b). The absolute amount of time spent vigilant was very similar between habitats ($F_{2,19}$=0.02, p=0.98, Fig. 6.1c) and the proportion of time devoted to vigilance did not differ between habitats (all ages: $F_{2,19}$=2.71, p=0.09, Fig. 1d, adults only: $F_{2,12}$=3.71, p=0.05), reflecting weak differences in time spent at GUDs between habitats, such that a slightly greater proportion of time was spent vigilant in shrub than tundra or shrub-tundra.

Factors determining time spent at GUDs

GUD was a good predictor of time spent at a trial. Habitat was not important in determining the time spent at a trial when considered in concert with GUD (w_+=0.03). Juveniles appeared to spend longer at trials for a given GUD than adults (w_+=0.93, Fig. 6.3a, Table 2) and required a greater amount of time foraging to achieve a similar GUD (Fig. 6.3b, Table 6.3). In general, lower GUDs required a greater total time at a trial and greater time spent foraging (Fig. 6.3, Table 6.2 and 6.3). However, individuals did not seem to increase time allocation to vigilance for lower GUDs. Instead, time allocation to vigilance appeared relatively constant across all GUDs. This trend was clear for adults, however juveniles appeared to have much more erratic time allocation to vigilance, as might be expected for inexperienced individuals. Further analyses were therefore repeated with just adults as well as both age classes, as juvenile and adult behaviour at GUDs appeared to differ.

Time allocation to vigilance

Temporal declines in vigilance were detected with increasing time spent at a GUD and are probably a major cause of observed habitat variation in GUD (Fig. 6.4, Table 6.5). These temporal trends did not differ between habitats. Investment in high cost vigilance increased over time and the extent of high cost vigilance was greater in shrub than tundra or shrub tundra (Fig. 6.5, Table 6.6).

Discussion

Arctic ground squirrels showed behavioural responses to differing habitat and visibility at both habitat and patch scales. Individuals appeared to adopt habitat-specific strategies to minimise predation risk. Details of behavioural responses to habitat and temporal trends in behaviour highlight some of the key factors that determine the extent of foraging costs between habitats. These details suggest that temporal trends in investment in vigilance appear quite consistent across habitats and are characterised by a high initial investment in vigilance. High initial vigilance is probably necessary to assess risk. The information gleaned from these behaviours may differ substantially between habitats based on visibility. The quality of this information may be reflected in quitting time, with individuals with lower quality information quitting at higher GUDs. This high initial investment results in relatively little variation in absolute time allocation to vigilance across different GUDs despite the fact that lower GUDs require a greater amount of time spent foraging. This is likely to increase the disparity in foraging efficiency between individuals which have low GUDs and those that quit patches with a greater amount of food remaining and may result in individuals in riskier habitat such as shrub having much reduced foraging efficiency relative to open habitats. GUD appears to provide the clearest picture of how habitat and patch visibility affects foraging behaviour, this may reflect the properties of GUDs as a more integrative measure of the total costs of foraging in a habitat (Brown 1999). However, fine scale time allocations may further elucidate the mechanisms which lead to these responses.

Habitat-level variation in GUD

GUDs showed clear variation between habitats (Fig. 6.1a). The higher GUDs observed in shrub are likely to be a result of reduced visibility and increased predation risk in these habitats. The more surprising result was the low GUD found in the intermediate shrub-tundra habitat. In this habitat, survival is low and population density is low, which suggests the habitat may be relatively low suitability. However, individuals have high mass, similar to that in apparently high-suitability tundra (Chapter 4). Individuals may forage more intensely than expected by predation risk alone due to state-dependent and external influences on marginal value of energy (Chapter 4). As GUD variation between habitats can be dependent upon predation, energetic and missed opportunity costs associated with foraging, as well as the effects of individual state upon these costs, it can be difficult to separate these factors (Brown 1999). In the case of shrub-tundra, there may be factors concerning individual state that drive this intense foraging (Chapter 4). As shrub-tundra is adjacent to open tundra, individuals may also benefit from social information concerning predation risk (Dall et al. 2005). This may be particularly advantageous where social information may be of higher quality than personal information. In this case, information from alarm calls in tundra may be a more accurate assessment of risk than personal information gained from vigilance in more obscured shrub-tundra as visibility is greater in tundra. In contrast to shrub-tundra, shrub habitats, which are more distant from tundra, clearly have much higher GUDs, which are likely to be associated with reduced visibility and increased predation risk.

Inter-patch variation in GUD

Foraging strategies to respond to patch-level visibility appear to differ between habitats (Fig. 6.2). In tundra, GUD was lowest where visibility was highest, suggesting individuals are less willing to remain at a foraging patch as visibility is reduced. In shrub-tundra there is relatively little response to local visibility with only a very weak increase in GUD with increasing visibility. In shrub, there is some evidence that individuals appear less willing to remain at a foraging patch with high visibility. These context-specific responses to patch visibility may reflect high costs imposed by local obstructions in a very high visibility habitat (Shrader et al. 2008; Baker and Brown 2010) compared to higher costs imposed by open patches in low visibility habitat. Where visibility is high at a broad scale, the benefit of high visibility for improving the ability of an individual to detect predators may considerably outweigh and potential benefits of local cover for avoiding detection, particularly as predators and prey will have different visual perspectives (Thetmeyer and Kils 1995). Avian prey and taller terrestrial prey may be considerably more able to see around small obstructions than an arctic ground squirrel, therefore local visual obstruction in a very open habitat may exaggerate inequities in chances of detection between predator and prey.

Conversely, being in high visibility patch may be more costly for prey in a low visibility habitat such as shrub or shrub-tundra. Here, habitat level obstructions may still impede visibility for predator detection, but the local high visibility may aid prey detection by avian and taller terrestrial prey. In shrub-tundra, a weaker trend was seen toward increased GUD as visibility increased, this may reflect similar processes as seen in shrub, although this is less pronounced given habitat visibility is somewhat higher.

Another factor which may help determine differing strategies in tundra and shrub is the nature of vegetation causing visual obstruction. In tundra, in many cases, reduced visibility was the result of tall graminoid vegetation obscuring visibility, whereas in shrub-tundra and shrub, visual obstructions were more often shrubs. The differing structural characteristics of these functional groups may have considerable effects on their potential role in obscuring overhead versus lateral visibility and their potential to act as barriers against avian attack. In thirteen-lined ground squirrels this seems to be the case, such that increases in vigilance were seen in response to lateral cover but not to overhead cover (Arenz and Leger 1997).

Time allocation in different habitats

Contrary to predictions, there were no differences in time allocation between habitats, either in total time spent at a GUD tray or for allocation to vigilance or foraging (Fig. 6.1b). Even though GUD in shrub was more than triple that observed in tundra or shrub-tundra, time spent at a GUD was reduced by less than 50%. This is surprising, given diminishing returns in food acquisition rate within a foraging bout were very likely, therefore higher GUDs would be expected to require much less time allocation.

Increased total time allocation was associated with lower GUDs, and appears to be largely driven by increases in time spent foraging, rather than any increase in vigilance (Fig. 6.3). Greater time allocation to predator detection was evident for juveniles when GUD was lower, but not for adults. This has also been reported for other sciurids, and may reflect increased vulnerability of juveniles to predation (Lea and Blumstein 2011).

In both demographic groups, individuals were required to forage for longer periods to achieve lower GUDs. Diminishing returns in food acquisition over time were largely caused by escalating increases in time spent foraging as more food is consumed which are likely to reflect a decrease in foraging rate over time. Relatively constant time allocation to vigilance regardless of GUD reduces the extent of diminishing returns associated with lower GUDs compared with that expected under a model of consistent vigilance over time. This pattern suggests individuals achieving higher GUDs may not be investing more in vigilance. This may reflect variation between individuals in vigilance behaviour and net foraging efficiency or a relatively invariant level of optimal time allocation vigilance at a patch. Despite current interest in individual variation in behaviour and personality in the field of behaviour (Dall et al. 2004; Dingemanse et al. 2010) and the potential for considerable impacts upon variation in GUD, these ideas have seldom been applied with respect to GUD. For example, bolder individuals may forage more intensively and have lower vigilance rates and therefore reduced GUDs.

Temporal changes in adult vigilance

Vigilance appeared to decline over time while at a foraging patch (Fig. 6.4). This may reflect increasing information acquisition as more time is spent at a patch. If, over time, no predator is observed during vigilance then perception of risk may decline resulting in reduced vigilance (Sirot and Pays 2011). These temporal declines in vigilance may contribute to relatively invariant time allocations to vigilance observed for different GUDs. Individuals that achieved lower GUDs therefore did not necessarily invest much more in vigilance as they continued to forage because most vigilance appears to occur at the start of a foraging bout.

Individuals in habitats with different visibility appeared to have quite similar temporal trends in time allocation to vigilance. This may have been driven by the nature of differences in predation risk between habitats. Physical structures, such as shrubs, can be assumed to create a long-term increase in background levels of predation risk via permanent reductions in visibility. As high risk situations become more lengthy, time and energy allocation to anti-predator behaviours are necessarily reduced (Lima and Bednekoff 1999). This may help to explain relatively similar behaviours between habitats that are likely to differ quite considerably in predation risk. Responses to direct predator cues of short duration in different habitats might be expected to differ more substantially between habitats than responses to differing background levels of risk measured in this study (Morrison 2011).

An alternate explanation may be that opposing forces of predation risk and efficacy of vigilance are determining allocation. Brown (1999) suggested a non-linear relationship between effectiveness of vigilance and investment in vigilance, with low vigilance expected when vigilance is either extremely effective or ineffective. If inefficacy of vigilance is driving vigilance lower in visually closed shrub habitat, this may counteract the influences of high predation risk.

Despite apparently investing a similar amount of time in vigilance and having similar efficiency at acquiring food during foraging behaviour, individuals in shrub appeared to acquire less food before quitting foraging patches. The costs of this initial investment in vigilance probably result in lower net foraging efficiency for squirrels foraging in shrub habitat. One reason for quitting at a higher GUD in shrub is that individuals are receiving lower quality information from vigilance behaviour due to visual obstructions impeding view. Individuals in open habitats are able to scan the environment at much greater distance than those in visually obstructed habitats; as such they may be able to achieve a better and more long-term assessment of risk. This could facilitate longer patch residency and lower GUD.

The difficultly in acquiring information in visually obstructed shrub habitat was demonstrated by the type of vigilance postures individuals engage in (Fig. 6.5). Individuals in shrub appeared to invest more in fully bipedal alert postures. These are likely to be more energetically expensive than head-up or hunched vigilance postures, but may be necessary in a habitat where visibility is poor, such that to achieve a sufficient line of sight individuals must elevate their eye-line. In the degus (*Octodon degus*), similar responses to vegetative cover have been observed, whereby rather than altering time allocation to vigilance in response to increased vegetative cover, individuals instead engaged in a greater proportion of bipedal postures (Ebensperger and Hurtado 2005). Increases in high cost vigilance postures with increased time spent at a trial may reflect greater energetic investment toward assessing risk when residency is longer.

Energetic costs

Multiple lines of evidence suggest foraging efficiency in shrub may be considerably lower than that in shrub-tundra or tundra. First, individuals appeared to quit at a higher density of food, and as such consume less food before moving to the next patch. This means that individuals in shrub more frequently had to spend time travelling between patches. Second, individuals with higher GUDs engaged in equal amounts of vigilance as those which consume more food. Given individuals in shrub generally had higher GUDs these individuals were probably experiencing a reduced foraging efficiency as a result of this high initial investment for a lower food return. Finally, individuals in shrub engaged more in energetically costly forms of vigilance, using bipedal vigilance postures more often than tundra or shrub-tundra individuals. Although this does not appear to have substantially affected foraging efficiency with respect to time, it may have imposed greater energetic costs, and further reduce the rate of net energy gain. In summary, foraging efficiency was lower in shrub, and this may explain the lower mass of individuals compared with shrub-tundra and tundra individuals, and lower survival than observed in tundra (Chapter 4).

Implications for increasing shrub cover under climate change

Densities of shrubs are expected to increase with warming climate (e.g. Myers-Smith et al. 2011), and my results suggest that the energetic cost of foraging for arctic ground squirrels may increase concomitantly. Although there may be some benefits of shrub cover in terms of providing a barrier against avian attack, these are more relevant at the patch scale within shrub habitats, rather than determining differences between habitats. Areas of dense contiguous shrub appear to impose particularly high foraging costs. These costs of foraging may be reflected at the population level and provide an explanation for the low mass of individuals and low survival in shrub habitat (Chapter 4).

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Table 6.1. Model selection of factors influencing giving-up densities. Top five models and null model are shown.

Model	AICc	ΔAICc	No. parameters	Model probability
habitat, visibility, habitat * visibility	81.22	0.00	7	0.44
habitat, visibility, habitat * visibility, CI	83.65	2.43	8	0.13
habitat, visibility, habitat * visibility, sex	84.28	3.06	8	0.10
habitat, visibility, habitat * visibility, age	85.25	4.03	8	0.06
habitat, visibility, habitat * visibility, time of day	85.55	5.02	8	0.05
Null	104.13	22.91	2	0.00

Table 6.2. Model selection of factors affecting the time spent at a foraging trial. Top five models and null model are shown.

Model	AICc	∆AICc	GUD (effect size, $\log_{10}(\text{sec})\text{g}^{-1}$)	Age (effect size, $\log_{10}(\text{sec})$)	No. parameters	Model probability
GUD, age	21.04	0.00	-0.13±0.03	0.40±0.15	4	0.38
GUD, CI, age	23.52	2.48	-0.15±0.03	0.42±0.16	5	0.14
GUD, visibility, age	23.76	2.72	-0.15±0.03	0.37+0.16	5	0.10
GUD, date, age	23.93	2.89	-0.13±0.03	0.38±0.16	5	0.09
GUD, sex, age	24.38	3.34	-0.13±0.03	0.39±0.16	5	0.07
Null	33.25	22.11			2	0.00

Table 6.3. Model selection of factors affecting the time foraging during a foraging trial. Top five models and null model are shown.

Model	AICc	∆AICc	No. parameters
GUD, age	24.94	0.00	4
GUD,	25.30	0.36	3
GUD, date	26.67	1.73	4
GUD, date, age	27.26	2.32	5
GUD, habitat	31.28	6.34	4
Null	41.72	15.78	2

Table 6.4. Model selection of factors affecting the time vigilant during a foraging trial. Top five models and null model are shown.

Model	AICc	∆AICc	No. parameters	Deviance
Null	53.00	0.00	2	11.61
GUD, age	54.14	1.14	4	9.42
GUD,	54.53	1.53	3	11.01
GUD, date,	57.43	4.43	4	10.94
GUD, date, age	57.53	4.53	5	9.42
GUD, habitat	58.64	5.64	5	9.91

Table 6.5. Model selection of factors affecting proportion of time allocated to vigilance for adult squirrels. The time only model performs better than one containing habitat.

Model	AICc	∆AICc	Model probability
Time	-39.27	0.00	0.92
Time, habitat	-32.67	6.60	0.03
Time, GUD	-31.52	7.75	0.01
Null	-31.13	8.14	0.01
Habitat	-24.62	14.65	0.00
GUD	-23.60	15.67	0.00
Habitat, GUD	-18.27	21.00	0.00

Table 6.6. Model selection for proportion of time devoted to high cost vigilance for adult squirrels, where high cost vigilance is defined as bipedal alert postures where an individual's back is straight.

Model	AICc	∆AICc	No. parameters	Model probability
Time at trial, habitat	-14.41	0	5	0.95
Habitat	-7.28	7.13	4	0.03
Null	-6.19	8.22	2	0.02
Time at trial	-3.91	10.5	3	0.00

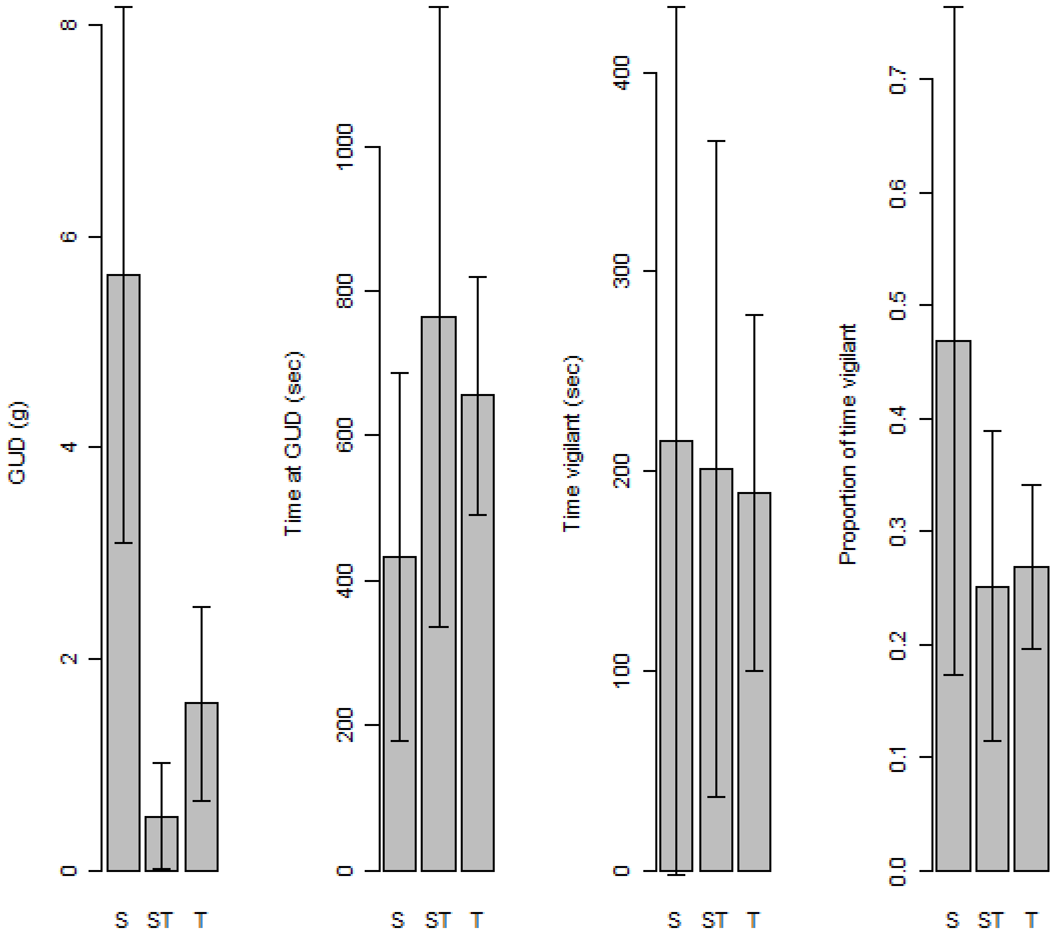

Figure 6.1. Differences in a) GUD, b) time spend at GUD trial, c) time spent vigilant and d) proportion of time spent vigilant between Shrub (S), Shrub-Tundra (ST) and Tundra (T) habitats. Values are mean ± 95% confidence interval.

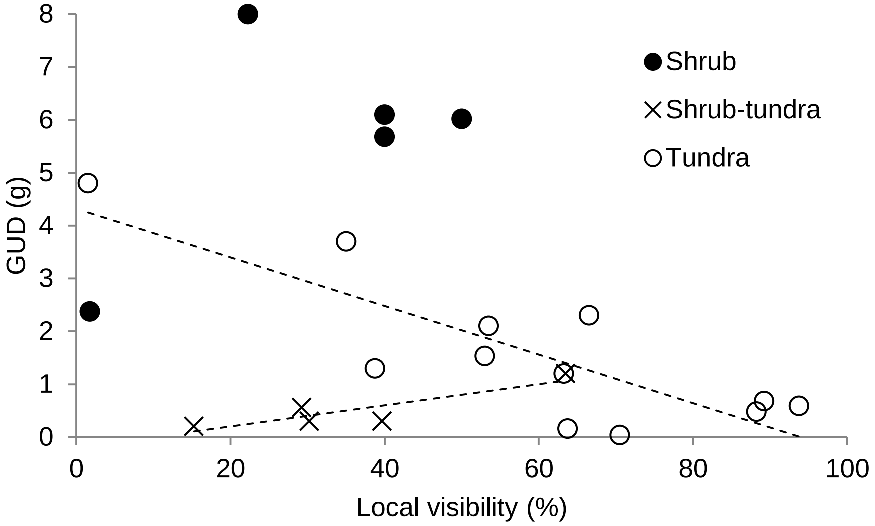

Figure 6.2. Relationship between local visibility to 10m and GUD in tundra, shrub-tundra and shrub habitats.

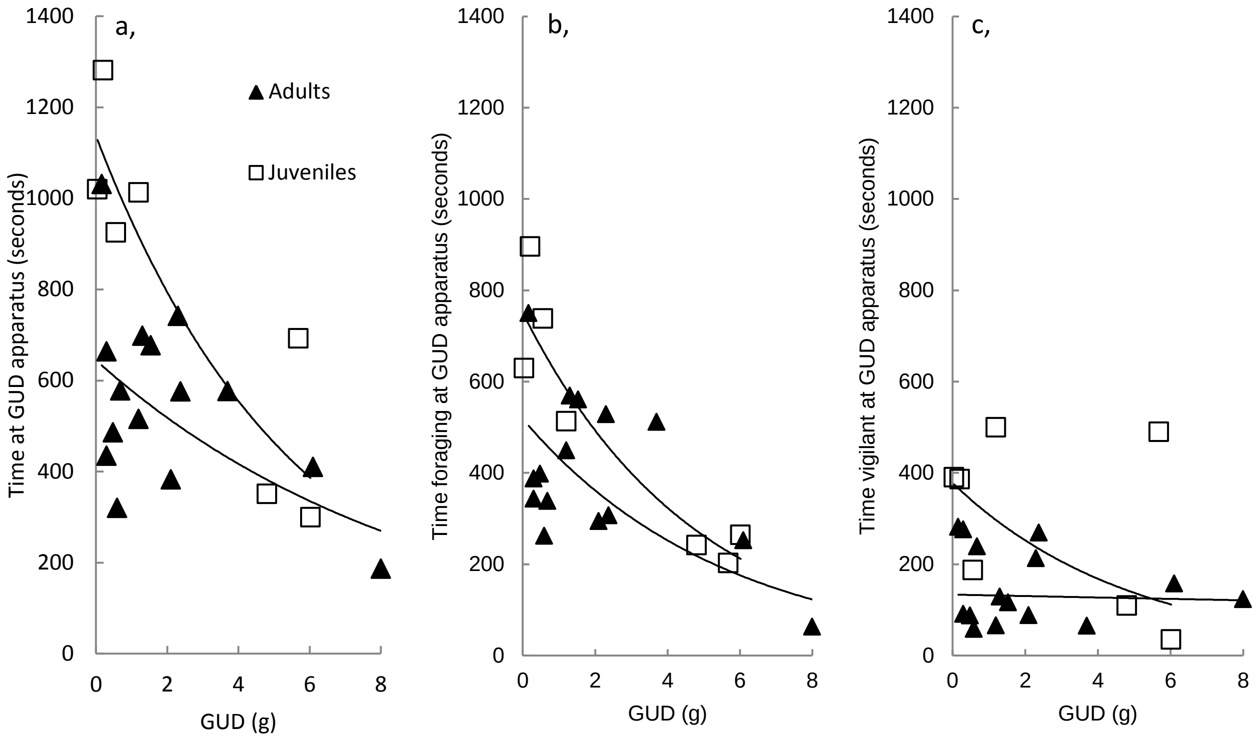

Figure 6.3. Effect of GUD and age of squirrel upon a) the total time spent, b) the time spent foraging and c) the time spent vigilant at a GUD trial.

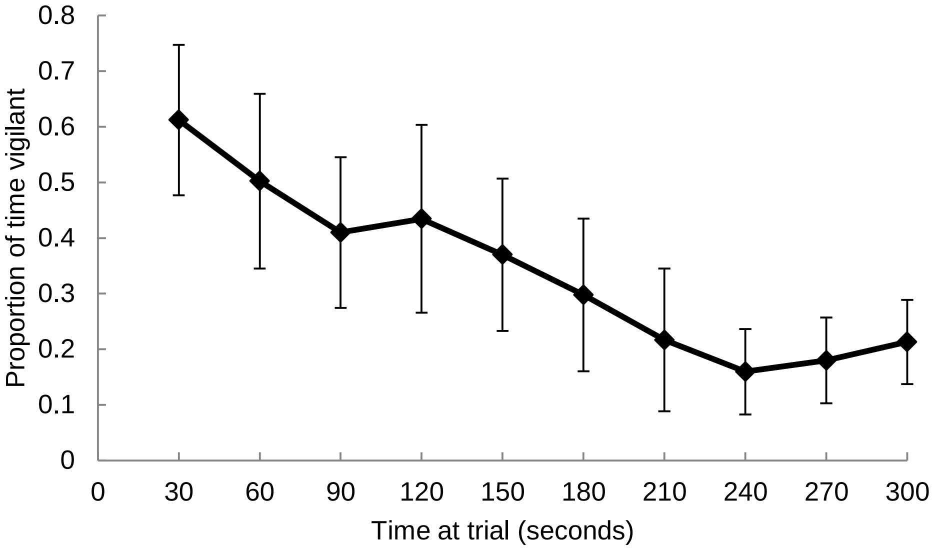

Figure 6.4. Temporal trends in proportion of time spent vigilant by adult squirrels during GUD trials. Values are mean ± 95% confidence interval.

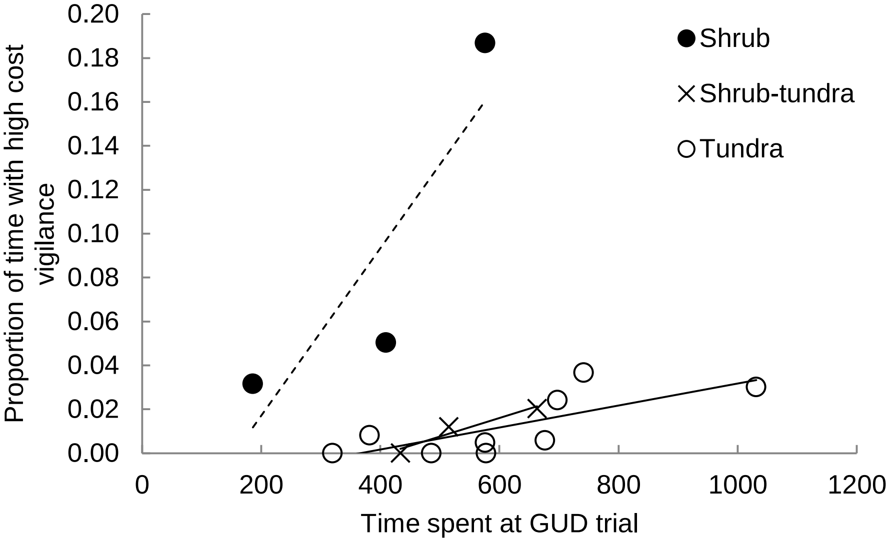

Figure 6.5. Effect of time spent at a GUD trial upon the proportion of time spent in high cost vigilance where individuals use bipedal, straight-back postures, in shrub, shrub-tundra and tundra habitats.

Chapter 7

Assessing the ecological factors that determine habitat suitability in changing environments for a northern herbivore foraging under predation risk

Variation in habitat suitability across heterogeneous environments can have a wide range of effects on species distribution, population dynamics, individual condition and behaviour. Persistence at the population and metapopulation level is dependent upon amount of habitat (Flather and Bevers 2002), configuration of different habitats (Akçakaya et al. 2004) and rate of change where habitats are in transition (Keymer et al. 2000). Individuals within metapopulations may be expected to differ in condition as a result of both patch suitability and density dependent effects (Pettorelli et al. 2002). In addition, variation in conditions between habitat patches may result in quite different behavioural strategies (Gillespie and Caraco 1987; Morris and Davidson 2000). These strategies affect individual condition, fitness, and ultimately survival and density at the population level, while movement of individuals between populations can have considerable consequences at the metapopulation level.

Habitat structure is one component of habitat suitability important to most herbivores. From the perspective of prey species, increased predation risk associated with certain habitat structures can reduce population growth by increasing direct mortality from predation; however, increasing evidence suggests substantial population effects are caused by behaviourally mediated changes in prey condition (Preisser et al. 2005). While it is difficult to demonstrate population effects of predator sensitive behaviour, there are now quite a few examples for different species (e.g. Hik 1995; Sinclair and Arcese 1995; Schmitz et al. 1997; Peckarsky et al. 2008).

The net effect of habitat visibility on predation risk for a herbivore represents the balance of costs of reduced ability to detect predators and benefits of being able to avoid detection by predators. Different species exhibit differing trade-offs along this spectrum (Kotler 1984). Where benefits from detecting predators are greater than those associated with avoiding detection, a series of behavioural and population responses to visibility are expected as obstructions on the landscape reduce visibility (Fig. 7.1a and c).

In this thesis I explored several factors affecting the distribution and abundance of arctic ground squirrels and the potential influences of climate induced environmental change on this species (Chapter 2). I then focused on differences between arctic ground squirrels inhabiting shrub, shrub-tundra and tundra habitats and considered the ecological factors determining distribution and population persistence across these habitats within a larger metapopulation. In order to do this I addressed the following five questions:

1. What ecological factors determine habitat suitability for arctic ground squirrels?

Throughout their distribution, a few core attributes have a substantial role in determining habitat suitability for arctic ground squirrels. These range from conditions where colonies are unable to establish to those limit long term persistence or simply may result in a habitat supporting only lower densities. Both long term conditions and frequency and intensity of certain events may affect habitat suitability. The spatial extent of these conditions and events is also likely to have a large impact on population responses. This can be demonstrated by considering how certain aspects of hydrology are likely to affect arctic ground squirrels (Fig. 7.2).

Sufficient soil drainage is essential for arctic ground squirrel occupancy (Carl 1971, Batzli and Sobaski 1980). In well drained areas with little flooding, with all other factors being equal, arctic ground squirrels should be able to establish and persist at relatively high densities. As the frequency of flooding, either from rainfall or rapid snowmelt, increases in intensity or extent, colonies may become restricted to favourable microhabitats and density may become reduced. With increasing consistency of flooding, eventually soils become fully waterlogged, and event initial establishment is inhibited. This has greater effect where waterlogging occurs over large spatial extents, such that arctic ground squirrels are excluded from large areas. Similar trends may be seen along other niche axes. Insufficient soil depth for burrowing where active layers are very shallow may also prevent occupancy (Chapter 2); the effects of this will be dependent on depth of thaw, spatial variability in active layer depth and interannual consistency in active layer depth.

Colonists of suboptimal habitat have been observed to be less likely to remain in these habitats the subsequent year (Carl 1971). Whether this represents mortality of these individuals or emigration is unclear. However, it is likely that these individuals represent those forced in to marginal habitat via density dependent competition. In the long-term, source-sink dynamics are probably evident and colonies in suboptimal habitat only persist due to immigration from other areas (Donker and Krebs 2011). As the relative distribution of habitats change, particularly if these sink habitats become more isolated, the potential for extinction at the population and metapopulation level may increase.

2. Do inferences from behavioural indices of habitat suitability correlate well with those derived at the population level?

Density and survival of adult female arctic ground squirrels were strongly correlated within habitats (Chapter 4). In addition, the apparently low suitability shrub-tundra (from the population perspective) also showed indications of being associated with more temporary habitat associations (Chapter 3). In contrast, giving-up density and individual condition were not consistent with predictions given the observed population processes. Notably, shrub appeared to be characterised by higher GUD, lower adult female mass (Chapter 4) and lower juvenile growth rates than shrub-tundra (Chapter 6), but had considerably higher adult female survival than shrub-tundra (Table 7.1). In addition, juvenile growth was lower in shrub than in shrub-tundra. The apparent difference between processes occurring at the individual and population levels has several potential explanations (Fig. 7.3).

One possibility for differences between responses to habitat at the individual and population levels relate to differences in individual state and payoffs from behaviours in different habitats. Intense foraging and high mass in shrub-tundra could be caused by nearby tundra affecting potential future payoffs for shrub-tundra individuals. Opportunities for colonisation of tundra might drive behavioural strategies to maintain competitiveness. Higher mass individuals tend to win territorial disputes (Watton and

Keenleyside 1974), therefore in order to be able to colonise tundra should the opportunity arise, individuals may maintain high mass.

Alternatively, the consistent differences between processes at the population level and individual characteristics might be an example of maladaptive behaviours of squirrels conditioned to tundra habitat entering shrub-tundra. High mortality and high immigration in low suitability habitat can reduce the potential for local adaptation. Lack of local adaptation in sink habitat has been described in other systems and may be important in this case (Anderson and Geber 2010; Battin 2004). Two quite disparate perspectives exist concerning source sink dynamics and the likelihood of maladaptive behaviour. While one view states lack of opportunity to adapt to sink habitats may be an increasing concern with increasing extent of, and more rapid environmental change (Caro and Sherman 2011a, b), the alternate is that plasticity in behaviour and learning are likely to reduce effects of genetic differences between individuals adapted to marginal habitat and those locally adapted to core habitat in source sink-systems rather than accentuate them (Kawecki 2008). In addition, many species appear to respond quite rapidly and adapt to altered environmental conditions (Schroeder et al. 2011). Marginal habitats may also favour the evolution of greater plasticity (Chevin and Lande 2011) allowing greater accommodation to local conditions.

The likelihood of maladaptive foraging behaviour in shrub-tundra will be dependent upon the extent of plasticity in foraging behaviour. Under this hypothesis, individuals residing in shrub habitat with higher fitness and would be expected to be more locally adapted to their habitat than individuals in shrub-tundra and hence exhibit very different individual traits. To assume such a great extent of variation in local adaptation between two habitats that probably both represent population sinks may be an overestimation of the differences between these habitats.

A more likely cause of maladaptive behaviour in shrub-tundra could be a perceptual bias causing individuals to respond to local cues from tundra as well as those in their core habitat. Certainly, due to the proximity of tundra to shrub-tundra, some cues from tundra will be experienced in shrub-tundra. For example, shrub-tundra individuals almost certainly hear vocalisations from tundra squirrels. In other systems social context seems to provide a route for transmission of information leading to maladaptive behaviour (e.g. Laland and Williams 1998; Nocera et al. 2006; Rieucau and Giraldeau 2011; Dubois et al. 2012). Perception of high squirrel density could possibly cause individuals to forage more intensively at the cost of high predation risk, in order to maintain competitive status. Other cues which might lead to perception of high density might be high numbers of transient individuals passing through the habitat. Alternatively, other cues from tundra may bias behaviour in shrub-tundra.

Differences in forage quality between habitats are another possibility, but seem less likely given the large difference between shrub and shrub-tundra, which are relatively similar habitats. High local forage value is expected to result in high missed opportunity costs (Brown 1999), causing higher GUD. If forage differences are driving differences between shrub and shrub-tundra, this would suggest that shrub had better forage. However, communities in shrub and shrub-tundra are quite similar and all other individual-based data is inconsistent with this as shrub is the habitat with slowest juvenile growth rates and smallest adult female mass.

In summary, behaviour and individual condition trends between habitats appear somewhat inconsistent with those observed at the population level, when all are considered simplistic indicators of habitat suitability. Differences most likely result from either differences in individual state between habitats that are not immediately obvious from population trends, or maladaptive behaviours in shrub-tundra. In both cases, the proximity of tundra to shrub tundra may have important implications for current behaviour and condition in shrub-tundra.

3. What role does predation risk have in determining population dynamics across the shrub to tundra ecotone?

Variation in giving-up density (GUD) between habitats indicated that costs of foraging differ between habitats, in particular between shrub and the less shrubby shrub-tundra and tundra habitats. Cost of foraging can include energetic, predation and missed opportunity costs (Brown 1999). It is unlikely that all the variation in GUD between habitats is explained by variation in predation risk, however variation this may certainly play a significant role in creating some of the observed differences. In particular, the difference in GUD between shrub and tundra may reflect contrasting predation risk. This is supported by fine scale behavioural data. There appear to be different foraging responses to local visibility in different habitats (Chapter 6). This suggests that visibility does affect predation risk at a local scale and implies that broader habitat level visibility also has a role in determining the strategy adopted to minimise predation risk at the local scale. Variation in GUDs between habitats are likely also partially affected by predation risk as a result of differing visibility, however these different cost of foraging are less easy to discriminate between at this level.

In shrub and tundra, both behavioural and population dynamics are consistent with expected trends if increased predation risk was altering predator sensitive and this was having effect on population dynamics mediated through individual condition (Fig. 6.1). In shrub, GUDs were high; this suggests individuals were leaving patches having consumed less forage. This has multiple costs; greater inter-patch travel time and energy investment in inter-patch movement to achieve a certain energy intake is expected as individuals only gain a low energetic reward at each foraging patch; in addition, squirrels appear to invest heavily in vigilance toward the start of a foraging bout and then investment declines over time. This means the costs of this initial investment will be greater relative to food consumed in shrub, where less food is consumed; finally, higher more costly forms of vigilance appear to occur in shrub than tundra. Lower foraging efficiency, as a result of these costs, would be expected to cause condition to be lower. This is seen with shrub individuals having lower mass than those in tundra and having slower juvenile growth. To scale to the population level, we would then expect the habitat with lower mass individuals to have lower survival, this was observed in shrub relative to tundra. This pattern suggests that increased shrub has negative effects on survival in part via indirect effect of predation mediated through changes in behaviour. Previous studies comparing boreal forest and tundra have suggested this is the case (Karels and Boonstra 1999; Gillis et al. 2005)

While the differences between shrub and tundra correlate very well with predictions if predation risk is a key driver of population dynamics, those in shrub-tundra do not. As previously discussed, this may reflect differences in individual state in shrub-tundra or be caused maladaptive behaviour in this habitat. Predation risk may still have an important effect on population dynamics, for example if intense foraging behaviour in shrub is maladaptive, this is because risk of predation becomes very high with intense foraging. This could be reflected in low survival observed in this habitat.

4. What are the relative roles of density and habitat suitability in determining population parameters and individual condition?

Given that density dependent and density independent processes have been shown to operate in concert on single population parameters (Karels and Boonstra 2000), it is difficult to quantify the often opposing roles of density dependence and habitat suitability on individuals and populations in the absence of density manipulations in a single habitat. Apparent lack of variation between populations may easily be misinterpreted as a lack of strong pressures when two strong forces have similar and opposing effects. For example, poor suitability habitat might be expected to cause reduced survival, reduced density and lower individual condition. However, if poor suitability habitats have low density, less strong negative density dependence is expected.

I found survival to be positively correlated to density, most likely as a result of both survival and density responding positively to habitat suitability. In addition, adult female mass and juvenile growth rate were positively correlated with survival and density, this again suggests these individual traits reflected habitat suitability directly to a greater extent than they were affected by density dependence.

Other factors appeared to show no clear association with density or apparent habitat suitability (from population processes). These included reproductive output and juvenile coccidial parasite load. Both of these measures represented quite coarse measures of the processes in question, which may mean subtle differences may not be easily discerned. However, given the direct effects of habitat suitability and that mediated via density act in opposing directions, an absence of difference between habitats does not necessarily mean neither process is operating, rather that either effects are relatively similar but opposing, or effects are minimal.

5. What models best represent distribution of individuals within a metapopulation where habitats vary in suitability?

I proposed three different models concerning the relationship between habitat suitability, fitness and population density:

A. Individuals in high suitability habitats have equal fitness to those in low suitability habitat, but high suitability habitat supports higher population densities.
B. Individuals in high suitability habitats have greater fitness and high suitability populations exist at higher density.
C. Density in low suitability habitat is equal or higher than that in high suitability habitat, however survival in low suitability habitat is very low.

Data in this study best supported model B, as demonstrated by the observed correlation between survival and density. If average fitness across individuals in a population is considered to be represented by the combination of survival and reproductive output, these results still appear valid. A further consideration of the proportion of females reproducing in each habitat would also aid this analysis.

Model B could emerge from two underlying processes. The first is an ideal despotic distribution (IDD, Fretwell 1972), which implies that individuals in the highest suitability habitats exclude less competitive individuals, which are forced to remain in lower suitability habitats which confer lower fitness. The second is that a habitat with increased survival causes density to become elevated (Hansson 1996). Although it is not possible to differentiate between these two underlying processes definitively, variation in dominance, which might give rise to an IDD, is likely amongst arctic ground squirrels. Territoriality has been shown in arctic grounds squirrels (Watton and Keenleyside 1974) and spacing behaviour has been suggested as a source of regulation in open alpine and tundra habitats (Carl 1971). Some properties similar to an IDD are therefore plausible from knowledge of behaviour.

Unlike population variables, which are consistent with an IDD, individual variables relating to condition suggest non-equilibrium dynamics may be important in this system. In particular, high female mass in shrub-tundra conflicts with some IDD predictions. In arctic ground squirrels, dominance is determined by mass (Watton and Keenleyside 1974). According to an IDD, the lowest suitability habitat is not expected to have high mass individuals. While certain aspects of an IDD may apply to arctic ground squirrel metapopulations across this ecotone, there is some evidence of either non-equilibrium dynamics or additional complexity than that described by the IDD model, perhaps due to payoffs associated with habitat-dependent local opportunities and future prospects for colonisation associated with the spatial configuration of habitat types.

Future shrub encroachment

I assessed the relative suitability of arctic ground squirrel habitats across a shrub to tundra ecotone in order to understand the potential implications of widespread shrub encroachment for future arctic ground squirrel, density, distribution and ecological role. It appears that shrubbier habitats are associated with lower survival and density and hence may tend more toward being population sinks than populations in open tundra. Surprisingly, intermediate levels of shrub appeared to support lowest densities and lowest survival in adult females.

One interpretation is therefore that early stages of shrub encroachment, where intermittent shrub patches establish, may quite drastically reduce population persistence. In this scenario, very considerable declines in density and distribution might be expected to the southern and lower elevation extents of squirrel distribution over relatively short timescales.

An alternative interpretation is that current dynamics across this ecotone partially reflect the spatial distribution of habitat types within the metapopulation. If this is the case, tundra still clearly represents the highest suitability habitat, with highest survival and density and individuals characteristics indicative of high suitability habitat. Differences between shrub-tundra and shrub however become less clear, and interpretation is dependent upon whether this is considered an equilibrium or non-equilibrium system.

In general this study suggests that increasing occurrence of dense shrub in the Arctic is likely to reduce densities and may restrict distribution of arctic ground squirrels. However, a number of other processes such as permafrost thaw may facilitate populations, particularly at the northern and high altitude extents of their range; the extent of this will be dependent on interactions with flooding and soil moisture. This thesis also highlights the value of considering behavioural, individual and population responses to habitat in order to obtain a fuller understanding of the complexities surrounding habitat suitability.

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Table 7.1. Summary of population, behavioural and individual responses to habitat in shrub, shrub-tundra and tundra habitats. Inferences made from these observations are shown in bold type.

	Shrub	**Shrub-tundra**	**Tundra**
Habitat suitability	**Intermediate**	**Low**	**High**
Survival (Adult female)	Intermediate	Low	High
Density (Adult female)	Intermediate	Low	High
Reproductive output	Equal	Equal	Equal
Costs of foraging	**High**	**Low**	**Low**
GUD	High	Low	Low
Individual condition	**Poor**	**Good**	**Good**
Mass (Adult female)	Low	High	High
Juvenile growth	Low	High	High
Juvenile parasite load	Equal	Equal	Equal

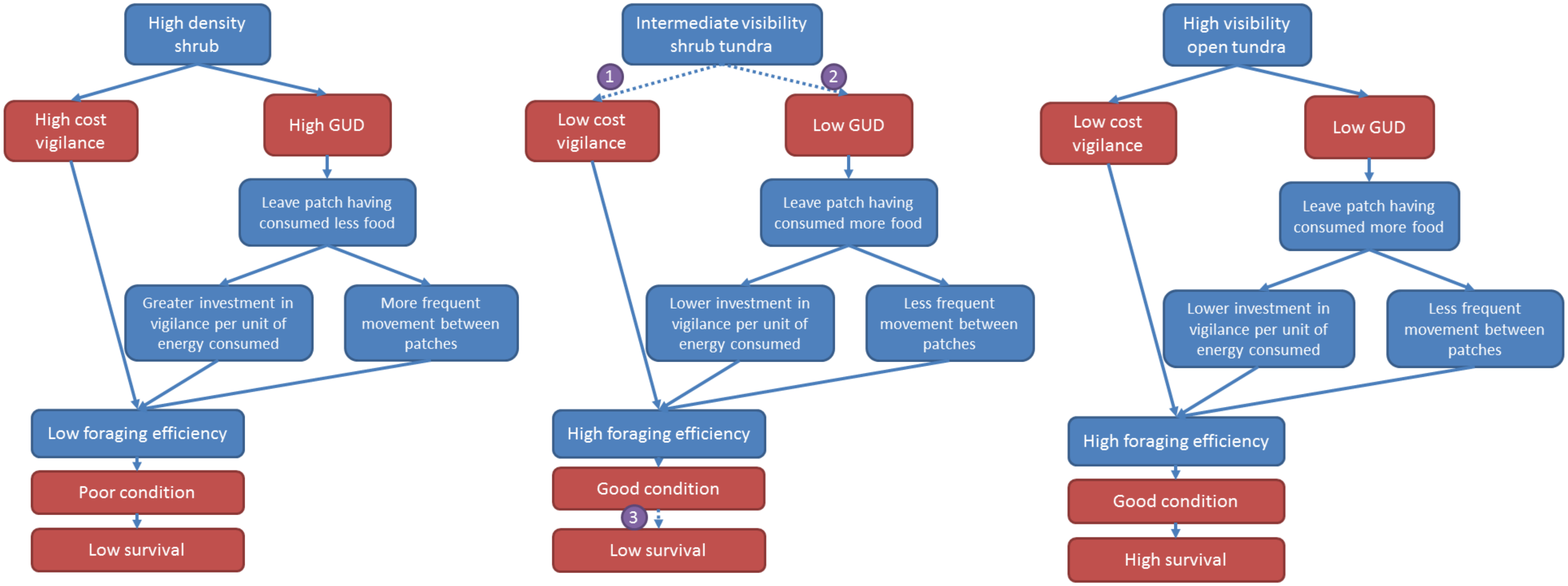


Figure 7.1. Diagram of the potential effects of shrub upon foraging, individual condition and survival. This diagram highlights a series of hypotheses as to why behaviour, condition and population dynamics appear to differ between shrub, shrub-tundra and tundra. In shrub-tundra processes contrary to predictions are denoted with broken arrows. 1) Intermediate density shrub results in investment generally low-cost vigilance postures such as head up postures compared to bipedal vigilance. This is surprising since shrub substantially reduces visibility in this habitat. 2) In shrub-tundra GUDs are generally low, suggesting low costs associated with foraging. This is surprising given predation risk was expected to be elevated in this habitat due to reduced visibility. 3) Good condition individuals appear to have low survival, this unexpected for direct effects of condition on survival.

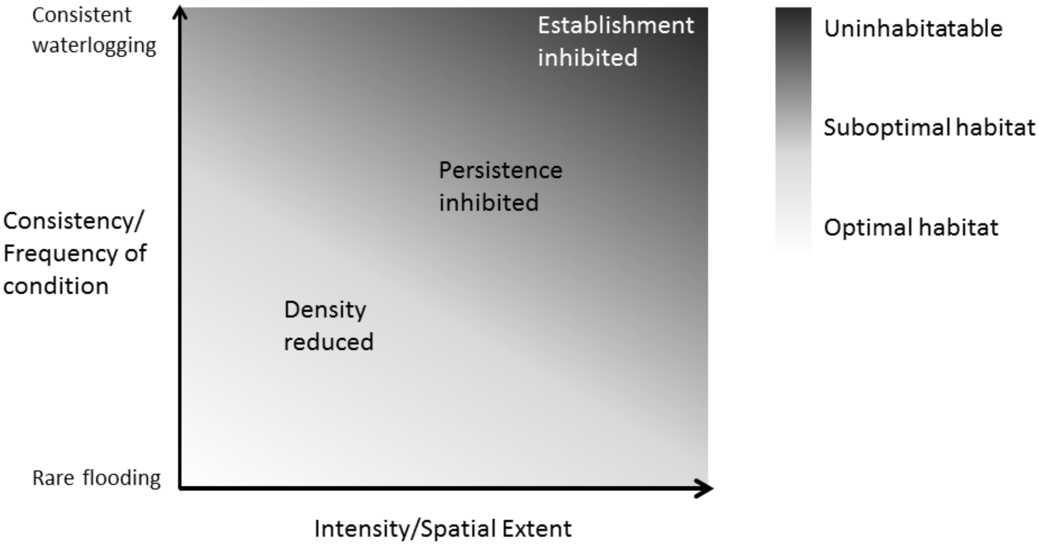
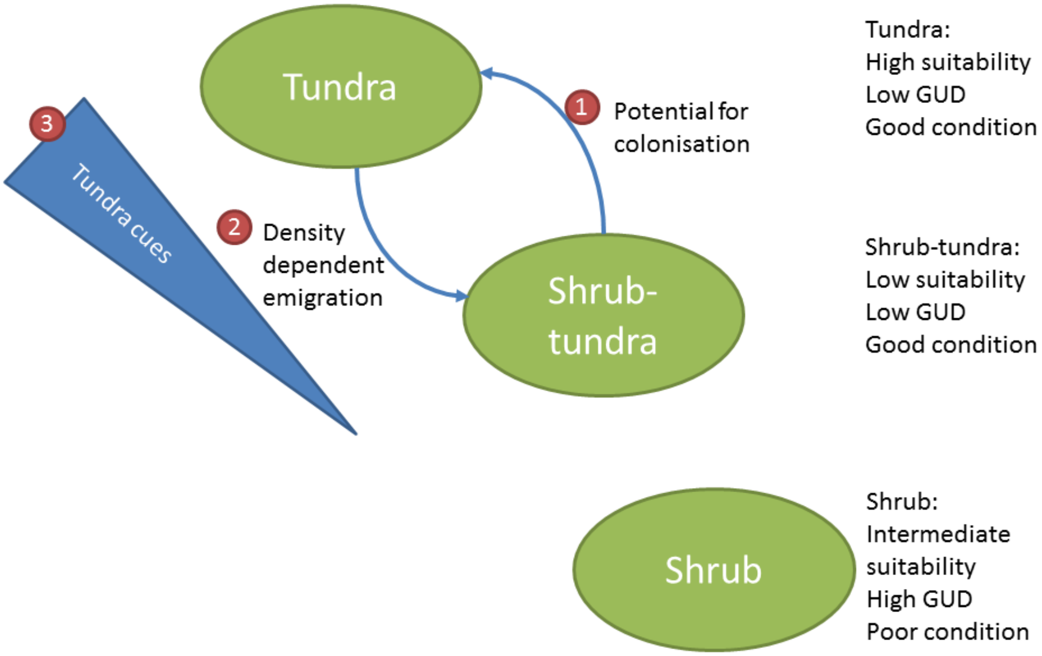


Figure 7.2. Effects of consistency and frequency of environmental stressors and intensity and spatial extent upon suitability of habitat. Effects of hydrology on arctic ground squirrel populations are shown as an example to demostrate the importance of these considerations.



① Shrub-tundra squirrels forage intensively despite high predation risk in order to achieve high masses and maximise chances of colonisation success in tundra.

② Tundra squirrels are forced out of tundra due to density dependent spacing. These individual have high mass (being from tundra) and do not adapt to new conditions in this sink habitat

③ Cues from tundra that are experienced in shrub cause maladaptive behaviour

Figure 7.3. Diagram of potential explanations for apparent inconsistencies between metrics associated with habitats suitability at the population and individual level in shrub-tundra.

Appendix: Influence of habitat visibility on post-emergence growth and pre-hibernation mass of juvenile arctic ground squirrels

Introduction

Body size in one of the best indicators of fitness for many species (e.g. Blanckenhorn 2000). In vertebrates, the conditions an individual experiences early in life can impact subsequent mass and lifetime reproductive success (Lindstrom 1999; Festa-Bianchet et al. 2000; Taborsky 2006; Hamel et al. 2009; Martin and Festa-Bianchet 2012), and for some species, individuals must reach a certain minimum threshold mass in order to reproduce at all (Frisch 1984; Naulleau and Bonnet 1996). Subsequent reproductive investment may also depend on mass or energetic reserves (Coté and Fest-Bianchet 2001; Crocker et al. 2001). In addition, survival increases with mass in many species and increased opportunities for individual growth can have positive population effects (e.g. in sciurids: Ozgul et al. 2010) and may increase population viability.

Even when yearling or adult mass is not related to juvenile growth and mass, indirect effects of poor growth during early development may occur. When poor initial growth is compensated for by accelerated growth at later stages, individual quality may be compromised, or survival probability may be reduced via engagement in risky behaviour to rapidly accumulate resources (Metcalfe and Monaghan 2001). Reductions in individual quality or survival probability may also be reflected in an individual having a reduced contribution to population growth.

Opportunities for maximizing juvenile growth often differ between habitats. Forage quality and availability, and predation risk determine the foraging opportunities for many juvenile herbivores (Gadallah and Jefferies 1995; McAdam and Boutin 2003). Once juveniles are able to forage with some degree of independence, the ability to rapidly accumulate energy will depend on foraging opportunities within a given habitat. However, habitats that provide favourable foraging conditions also regularly support greater herbivore population densities. Juveniles will often be subdominant to older individuals and therefore may experience particularly reduced foraging opportunities in favourable habitats as high densities promote high competition. When considering the effects of habitat on juvenile growth, it is thus necessary to consider the opposing effects of environmental quality and competition for food.

In addition to environmental variation in growth rates, variation in growth rates and subsequent body size between sexes are common (Fairbairn 1997; Badyaev 2002). Where sexual dimorphism is male biased, selection may be driven by males gaining greater reproductive advantages from higher mass than females. Sexual selection for competitive males can select for higher mass males and increase variation in reproductive success associated with mass for males relative to females. However, increasingly diverse reasons why male reproductive success may show a greater response to mass than is observed for females are being acknowledged, such ability to protect young from infanticide (Isaac 2005). This increased selective pressure on mass may cause higher growth rates in males and more risky strategies to accumulate mass than for females.

Arctic ground squirrel foraging decisions and mass gain are likely to be strongly related to visibility within habitats. Favourable habitat for arctic ground squirrels in alpine areas appears to be associated with high visibility; these high visibility habitats are likely to become reduced as a result of climate change (Wheeler and Hik 2012). Reproduction, active season survival and growth rates were greater in an alpine tundra than in a lower visibility boreal forest population (Gillis et al. 2005), and there was evidence of increased stress in boreal populations than those in the alpine (Hik et al. 2001). Boreal populations also appear to have lower density and survival than those in meadow habitats (Donker and Krebs 2011; Donker and Krebs 2012), which may also confer greater visibility than boreal forest. Further, in boreal forest, arctic ground squirrel burrows were more likely to be located in high visibility areas and high visibility was associated with longer term burrow occupancy (Karels and Boonstra 1999).

The ability for arctic ground squirrels to detect predators may also be a key component of habitat quality. Climate change is causing shrub encroachment on to previously more open arctic and alpine tundra (Sturm et al. 2001; Tape et al. 2006; Elmendorf et al. 2012; Myers-Smith et al. 2011), and has the potential to alter habitat for arctic ground squirrels. As shrub encroaches on open tundra, visibility and ability to detect predators is likely to become reduced. Many herbivores alter behaviour to reduce predation risk, and in doing so often experience other costs such as foraging efficiency (Lima and Dill 1990; Lima 1998). While predator-sensitive behaviours may reduce predation mortality, investment in predator sensitivity may reduce growth rates and mass. Such reductions in mass and growth may have implications for lifetime reproductive success.

Arctic ground squirrels are a hibernating rodent for which growth rates and juvenile mass prior to hibernation are likely to have a high impact on later reproductive success. The magnitude of relationship between mass and reproductive success may also differ between sexes. Sexual differences in variation in reproductive success have been reported for ground squirrels, with males having more variation in reproductive success than females (Jones, Van Zant, and Dobson 2012)

For female ground squirrels, reproductive success, in particular, offspring mass, and litter mass has been linked to maternal condition and energetic reserves (Dobson 1995; Risch et al. 2007; Skibiel et al. 2009; Murie 2009) and in European ground squirrels low mass females show delayed oestrus (Millesi et al. 1999). For male arctic ground squirrels, the effects of juvenile mass on reproduction may be even greater. Male competition for mates in spring is particularly intense for arctic ground squirrels and is associated with substantial loss of mass (Buck and Barnes 1999), stress, injury and mortality (Boonstra et al. 2001; Delehanty and Boonstra 2011). To survive the mating period it is likely that prior energetic reserves must be high. In addition, higher mass individuals appear dominant in arctic ground squirrels (Watton and Keenleyside 1974), and may obtain greater opportunities for mating and be exposed to less risk of negative outcomes of competitive interactions. Lifetime reproductive success is therefore likely to be greater for male arctic ground squirrels of greater mass.

I assessed the effect of visibility and local adult population density on post-emergence growth and pre-hibernation mass for juvenile arctic ground squirrels. I considered the effect of habitat on growth rate in terms of habitat quality with respect to foraging conditions and also local density of adults that will determine competitive interactions. I also considered how sexual differences in juvenile growth in these habitats and the potential effects of the differing life history constraints for males and females. The following three hypotheses were addressed:

1. Juvenile growth rates and pre-hibernation masses will be greater in habitats where visibility is higher. Higher visibility habitat should confer reduced predation risk for juvenile arctic ground squirrels, as predators can be detected at distance. As a result, there should be less need for investment in predator sensitive behaviours and therefore greater foraging efficiency, greater growth and higher pre-hibernation mass.
2. Where there is a high local density of adults, juvenile growth and pre-hibernation mass will be reduced as a result of competitive interactions with these adults.
3. Males will have higher growth rates and greater masses than females as a result of stronger selection on mass. High mass in males may increase competitive abilities and ability to protect young from infanticide. In addition, due to low survival, males may adopt a more r-selected reproductive strategy such that reproductive success as a yearling comprises a greater proportion of lifetime reproductive success. These factors are likely to contribute to a greater selective pressure on male mass than female mass.

Methods

Growth rates and pre-hibernation masses

Growth rate and pre-hibernation mass were assessed following the procedures outlined in Chapter 5, for all habitats in both 2008 and 2009. The relative importance of local population density, year, and visibility at two scales; the habitat scale and also locally, associated with activity areas of the each juvenile were assessed upon both early growth and pre-hibernation mass. Trends were assessed separately for males and females. All possible combinations of variables were compared using AICc and relative importance of variables in determining each of early growth and late September mass were assessed using Akaike weights. Linear regression was used to assess the relationship between post-emergence growth rate and pre-hibernation mass for males and females separately.

Variables affecting mass and growth

Mean visibility to 25m across the site in which a juvenile was found was assessed using line of sight measurements as outlined in Chapter 4. Local habitat visibility associated with areas of activity for each juvenile was also by estimating the mean visibility to 25m across all locations in which an individual was found during trapping, weighted by the frequency of capture in each location. During a trapping session an individual could be trapped at multiple locations in a given day. The probability of recapture at a location may be reduced by recent activity of researchers in the area, therefore the location of initial capture may be disfavoured in recaptures. The initial capture was therefore more likely to represent a highly selected location than recapture locations. Recaptures provided important information regarding extent of movements but the location of recaptures may be contingent on aversion to the initial location of capture. All recaptures after the initial capture in a given day were weighted to half of that of the initial capture to account for this potential difference in preference.

A local density index of adult squirrels was estimated by determining the number of adult individuals trapped within 50m of the each location at which a juvenile was trapped. Frequencies of local adults were assessed for each grid location by counting the number of individuals trapped in the focal and adjacent trap locations. The mean local density experienced by a juvenile was then assessed in a similar manner to local visibility; for each time a juvenile was trapped, the local adult density at that location was taken multiplied by the weight for that trapping event (1 for initial captures, 0.5 for recaptures), this was then divided by the sum of all weights.

Local adult density estimates for each juvenile were adjusted to correct for underestimation of local density of adults when juveniles used habitat on the edge of study grids. When trap locations were on grid edges, they had fewer adjacent traps and therefore the number of local adults was likely to be underestimated. The extent to which juveniles used edges of grids was assessed by assigning each juvenile with an edge score. The edge score was the average number of traps surrounding each of the locations the juvenile was trapped, weighted by the frequency of capture at each location, multiplied by the weight according to whether that capture was an initial capture or recapture. Individuals without any captures on the edges of grids (referred to as central juveniles herein) were then identified using their edge score (maximum edge score = 4). Second order jackknife resampling techniques with removal of random trap locations were applied to data for central juveniles to assess the effect of being trapped at the edge of the grid upon estimates of local adult density. Data were simulated with two random trap locations removed from the grid, edge score was reassessed for all these individuals, and local adult density calculated. This was repeated with replacement over 25 iterations for each grid.

Initial analyses of data showing a reduced edge score as a result of trap removal was then used to fit a model to estimate the original local adult density with all edges present based upon the edge score and measured local adult density under trap location removal. The final model incorporated a correction factor based on edge score to be applied to measured adult density and to the square of local adult density as well as a linear effect of local adult density (for which the effect size was ≈ 1, effect size=0.96). Incorporating the locations a juvenile was trapped in to the model caused little improvement in fit for the additional parameter and therefore was omitted (ΔAICc=559.9). Removal of any other parameter caused an increase in AICc so all other parameters were retained. The final correction model explained a high proportion of variation in the resampled data (R^2=0.98). The correction model was applied to the original data where edges were missing to produce final estimates of local adult density. For growth data, mean visibility and local adult density were derived from July trapping data. To assess their effect on pre-hibernation mass, mean visibility and local adult density were derived from July and August trapping data.

Results

Growth rates

Both males and females growth were positively associated with habitat visibility (Fig 1., Table 1). For both males and females, the model with greatest support had habitat visibility alone affecting growth rates (Table 1). Habitat visibility had strong support across the model set (Females: w_+=0.66, Males: w_+=0.80). Growth rates were slightly greater for males than females (Fig. 1). Broad habitat-scale visibility appeared to be more important than local visibility experienced by a squirrel in determining growth rates (ΔAICc=1.7 for females and ΔAICc=4.4 for males). There was little evidence of any effect of local density of neighbouring adult squirrels on juvenile growth rate or any difference in growth between years.

Pre-hibernation mass

The relationship between pre-hibernation mass and visibility was different for males and females. Female masses showed a positive association with habitat-scale visibility (w_+=1.00), but also appeared to show some negative effects of visibility more local to the focal squirrel (w_+=1.00). Visibility did not appear to affect male pre-hibernation mass despite having quite strong effects on growth rates (Table 2, habitat visibility: w_+=0.05, local visibility: w_+=0.08). The weak relationship in males may be partly a result of two juveniles at one site with low pre-hibernation mass, if these are removed the effect of visibility upon mass becomes very similar to that seen in females.

Growth rate and pre-hibernation mass

The association between growth rate and subsequent pre-hibernation mass differed between males and females. For females, high growth rates appeared to result in high mass prior to hibernation ($F_{1,12}$=5.22, p=0.04), however male September mass appeared to be independent of growth rate ($F_{1,6}$=0.01,p=0.93). This was true even when the two males with low mass relative to visibility were removed.

Discussion

Effect of visibility on juvenile growth and mass

Visibility at a broad-scale appears to have positive effects on early growth rates for juvenile arctic ground squirrels, but the local density of potential dominant competitors did not have substantial effects on growth. For both males and females, higher post-emergence growth rates were observed in higher visibility habitats. Habitat quality with respect to visibility therefore appears more important than intra-specific competition in determining juvenile growth.

High growth rates in high visibility tundra habitat may reflect a reduced risk to young juveniles when ability to detect predators is greater. In foraging species, there is often a trade-off between avoiding being seen and detecting and evading predators early. In ground-dwelling sciurids, preference for foraging areas with elevated visibility has been demonstrated (Carey 1985) and less resources are devoted to predator detection in these habitats (Sharpe and van Horne 1998; Mateo 2007). However, relationships with cover can be complex, with benefits of cover depending on its structure and relative value as protective cover and cost as visual barrier (Hannon et al. 2006). Results from this study suggest that for juvenile arctic ground squirrels, poor visibility results in reduced growth rates. Risk of predation in low visibility habitat may also reduce foraging efficiency due to greater need for predator sensitive behaviours.

Whether predator sensitive behaviours are instigated solely by juveniles or a response to parental cues is unclear. During early development, when young juvenile ground squirrels are foraging, they often remain in close proximity to burrow refuges and mothers also remain in close proximity assessing potential risks. Frequent calling from adults is observed during this period (pers. obs.). In such a situation, where parents and vigilant and burrows provide nearby refuges in which to hide, it is highly likely high visibility would be advantageous to this species as indicated by this study.

Contrary to predictions there was no effect of local density detected upon juvenile growth rate. This may indicate an absence of competition for food between juvenile and adult ground squirrels due to differing resource needs or a lack of forage limitation. Adults may also contribute to vigilance and predator detection so that predation risk is lowered in high density areas. This benefit may counter any costs of competition. Overall, high visibility habitat, which is presumably high quality, appeared to have higher growth rates, individuals in these habitats did not appear to be negatively affected by high local density of adults.

Implications of growth and mass responses to visibility

Differences in growth observed in arctic ground squirrels caused by natal habitat may have implications for lifetime reproductive success. Where juveniles are philopatric (mainly females) this may be reflected in population processes in the natal habitat. Where juveniles disperse (males and females) the long-term effect of juvenile growth could affect population processes in the new habitat. An individual contribution to persistence at the population and metapopulation level can be related to its early experiences.

In ground squirrels, many life history traits depend on mass (Dobson and Michener 1995; Millesi et al. 1999; Risch et al. 2007; Skibiel et al. 2009). The trade-off between investment in current and future reproduction has been well described in many species. Individuals with lower mass or energetic reserves may forgo reproduction in a given year where their reproductive success is likely to be low. Reproduction is forfeited in favour of maximising survival and energy gain to invest in reproduction in following years. While the tactic of not reproducing due to low mass may represent the best tactic for an individual, individuals that forgo reproduction as yearlings may still have lower lifetime reproductive success than heavier individuals which are able to reproduce in their first year. Juveniles accumulating insufficient resources prior to hibernation may be less likely to reproduce as yearlings and may therefore have lower lifetime reproductive success.

Ground squirrels mass is also positively associated with overwinter survival (Murie and Boag 1984; Lenihan and Vuren 1996). Juveniles gaining insufficient mass to survive hibernation or other energetically costly life events will not contribute to population growth and will have lifetime reproductive success of zero. Given the fitness costs a failing to survive to reproductive maturity are so high, it might be expected that rather than follow growth trajectories towards below-survival-threshold masses, individuals would be willing to engage in more risky foraging behaviour. This may limit the minimum growth rate in more risky habitats. Certainly for males, the growth rate response to visibility appears curvilinear, which may suggest such processes are important.

Local visibility may also have an additional role in governing predation risk. For females, differences in mass associated with visibility are also reflected later in development, as seen by the positive association between visibility and pre-hibernation mass. While high visibility appeared to be advantageous at the broad scale, more locally there was an apparent benefit of increased female mass associated with lateral visual obstruction. This may reflect both the benefits of cover in terms of visibility, and also the structural barrier provided by vegetation, which may reduce the risk and also success of avian attack on juveniles. The local protection provided by shrub cover may have a greater benefit than the potential costs such as slowed escape movement found in other species of ground squirrel (Schooley et al. 1996).

Sexual variation in response to visibility

Male growth rates showed a greater response to visibility than female growth. Males in the highest visibility habitat had particularly high growth rates. The strong male growth response to visibility may reflect the greater need and payoff for males to gain mass (Fig. 4), and therefore a tendency to increase foraging rates substantially in optimal conditions. However, the strong male growth-response to visibility may also reflect additional risks associated with visibility important only to males.

Mass upon hibernation for juvenile male arctic ground squirrels is likely to be an important determinant of lifetime reproductive success. Greater pressures on male arctic grounds squirrels associated with high costs of both dispersal and particularly reproduction are evident from behaviour (Holmes 1977), hormonal and physiological indicators of high stress (Boonstra et al. 2001; Buck and Barnes 2003; Delehanty and Boonstra 2011), mass loss during breeding and dispersal (Buck and Barnes 1999) and high mortality (Boonstra et al. 2001). Given almost all yearling squirrels breed and male aggression, injury and mortality are high during the mating period (Boonstra et al. 2001), a male yearling's breeding season may represent the only opportunity for reproduction. Dominance appears to be related to mass in this species (Watton and Keenleyside 1974) and is not only likely to determine reproductive success but also influence breeding season survival, therefore lifetime reproductive success is likely to be highly associated with yearling mass in this species.

Individuals may also gain benefits from growth in terms of reduced mortality risk from infanticide. Infanticide has been reported in arctic ground squirrels and adult males may pose a greater threat to juvenile males than females. In other species of ground squirrel, where infanticide is well-documented, the majority of infanticide appears to be committed by females on unrelated juveniles, most likely for nutritional benefits (Trulio 1996; Stevens 1998). However in arctic ground squirrels, unrelated males are the main cause of infanticide, and infanticide appears to be a result of males establishing new territories in the area (McLean 1983). For both male and female juveniles mortality from infanticide has been observed, however greater risk may accrue to juvenile males which would be direct competitors to the incoming male in the next summer.

Differences in growth responses to visibility may reflect differing relationships between mass and expected lifetime reproductive success for males and females. Males are likely to have a higher threshold mass for survival from entering hibernation to the end of the mating period than females (Fig. 4). In addition, males may experience greater reproductive gain from high mass than females (Fig. 4). Therefore, males may have the strongest pressures to attain to attain a threshold mass and higher pay-offs from high mass prior to hibernation.

Temporal changes in growth

Males and females may experience different pressures and constraints, causing different temporal growth responses to condition. While females appear to respond consistently to broad-scale visibility, males apparently only show reduced growth in response to low visibility during the earlier stages of development and pre-hibernation mass was independent of early growth.

Subsequent to emergence, juveniles remain strongly associated with natal litters, responding to maternal vocalisations (pers. obs.). Opportunities for divergence from behaviour of littermates at this point may be costly, potentially leaving a single juvenile exposed. Although males show higher growth rates and stronger responses to visibility than females early in development, there may be limits to the extent to which mass gain can differ between sexes. As juveniles become more independent, differing pressures may be more evident in mass response to visibility of juveniles.

While female pre-hibernation mass is associated with female post-emergence growth, for males these two variables appear independent. Given males are likely to have a higher rate of return of fitness with mass gain, males may compensate for poor early growth by compensatory growth later in development. Attempts to achieve compensatory growth are the most likely explanation for the lack of correlation between post-emergence male growth and pre-hibernation male mass. Where attempts succeed, individuals would be expected to show elevated mass; where the costs of compensatory growth (increased predation risk, increased competition) cause such attempts to fail, mass may be much lower. Given such costs are stochastic this is likely to increase variability in pre-hibernation mass in males.

Compensatory growth is often costly. Juvenile thirteen-lined ground squirrels, have been shown to compensate for a low energy food source with increased investment in foraging, however they also showed reduced vigilance relative to those fed on a high energy food source, which attained higher mass (Arenz and Leger 1997). In addition to increased predation risk, costs of compensating for low growth rates later in development include changes in tissue quality and energetic stores. (Metcalfe and Monaghan 2001), which may be particularly important for hibernating mammals, and ultimately, compensatory growth may lead to increases in mortality (Johnsson and Bohlin 2006). This may explain the lesser extent to which females appear to make up for low post-emergence growth.

Implications for shrub encroachment

Increased shrub encroachment associated with warming has the potential to lead to negative effects on juvenile growth. Juvenile arctic ground squirrels had lower initial post-emergence growth rates in low visibility habitats. These were reflected in lower masses prior to hibernation in juvenile females but not juvenile males. Reduced mass in female ground squirrels has been associated with reduced reproductive output (King et al. 1991; Neuhaus 2000). Reduced mass as a result of changes in foraging associated with reduced visibility as shrubs encroach could result in reductions in reproductive output and population growth rate. As shrub densities increase, effects may also be seen on competitive relationships, quality and longevity. These effects may be caused both reduced mass in lower visibility habitat and increases in risky foraging to compensate for poor growth early in life, and increased compensatory growth affecting quality and composition of tissues.

For juvenile females, local shrub appeared to confer growth advantages, possibly by increasing safety from avian predators. Low densities of shrub may therefore be advantageous, providing safety if burrow systems are established in their vicinity. However, as shrub densities increase, as projected with warming and visibility becomes reduced on the broader scale, losses in visibility at this broad scale are likely to be the more influential factor, reducing juvenile growth.

Overall, increased shrub density reduced early growth of juvenile arctic ground squirrels and pre-hibernation mass of female juvenile arctic ground squirrels. This was most likely a result of increased predation risk from predators and potential increased risk from unrelated conspecifics. Reduced growth in low visibility habitats suggest individuals forage less intensively in these habitats, possibly as a response to increased predation risk. In addition individuals may be forced to adopt more risky foraging strategies to compensate for mass deficits later in the season.

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Table A.1. Top 5 models selected using AICc that show an improvement over null models and null model explaining effects of broad habitat visibility, local habitat visibility, local adult density and year upon a) male and b) female juvenile growth after emergence from natal burrows.

a) Male juveniles

Parameters	AICc	ΔAICc	No. parameters
Habitat visibility	-5.99	0.00	3
Habitat visibility, year	-5.10	0.88	3
Habitat visibility, local adult density	-3.64	2.35	4
Null	-3.02	2.97	2
b) Female juveniles			
Habitat visibility	-19.52	0.00	3
Local visibility	-17.84	1.68	3
Habitat visibility, local adult density	-17.43	2.10	4
Local visibility, habitat visibility	-16.96	2.57	4
Habitat visibility, year	-16.94	2.58	4
Null	-15.89	3.63	2

Table A.2. Top 5 models selected using AICc and null model explaining effects of broad habitat visibility, local habitat visibility, local adult density and year upon female juvenile growth pre-hibernation mass.

Parameters	AICc	ΔAICc	No. parameters
Local visibility, habitat visibility	126.48	0.00	4
Local visibility, habitat visibility, local adult density	131.70	5.22	5
Local visibility, habitat visibility, year	131.91	5.42	5
Local visibility, habitat visibility, local adult density, year	139.08	12.59	6
Habitat visibility	142.81	16.33	3
Null	149.27	22.78	2

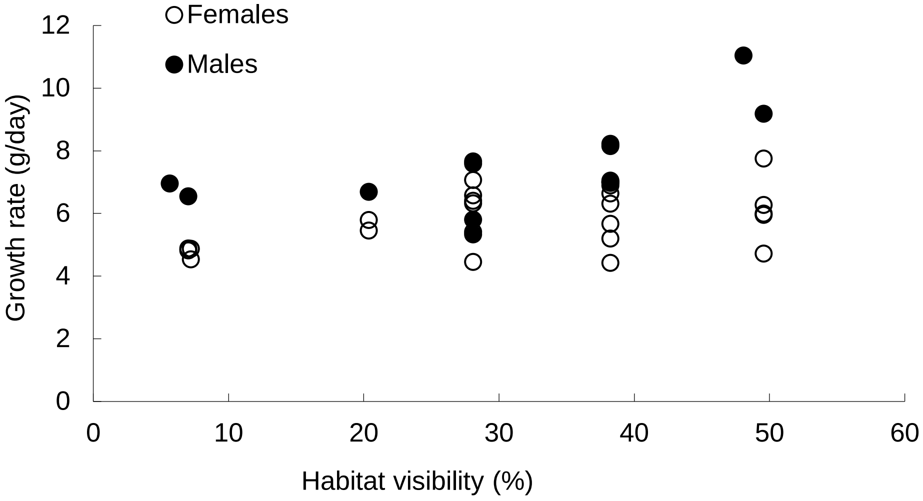

Figure A.1. Relationship between visibility at the broad habitat level and post emergence growth rates of male and female juvenile arctic ground squirrels.

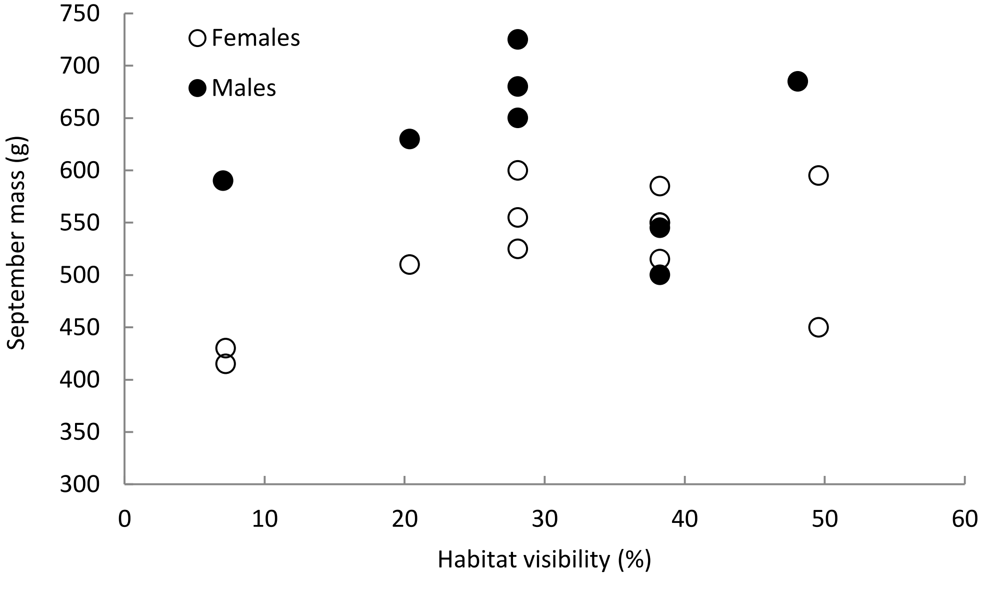

Figure A.2. Relationship between broad scale habitat visibility and pre-hibernation mass of male and female juvenile arctic ground squirrels.

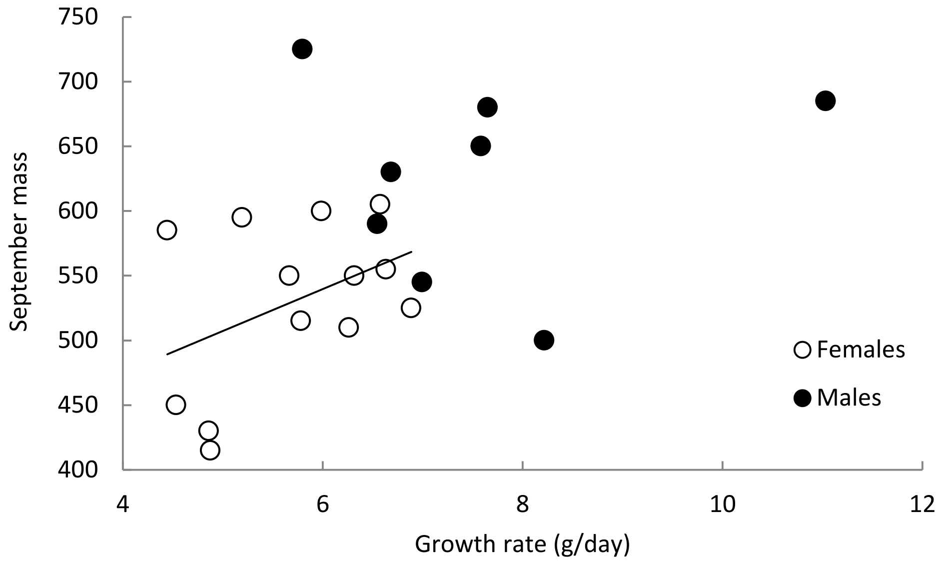

Figure A.3. Relationship between post emergence growth rate (between emergence in July and early August) and pre-hibernation mass in male and female juvenile arctic ground squirrels. Regression line is shown for females. No strong association was observed for males.

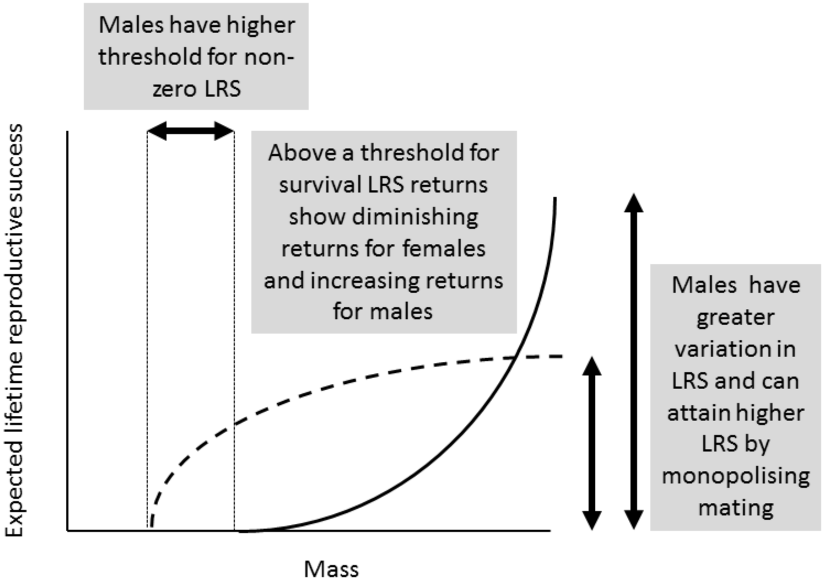

Figure A.4. Hypothetical relationships between mass and expected lifetime reproductive success for male and female juvenile arctic ground squirrels.