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Influence of shrub canopies on growth rate and pre-hibernation mass of juvenile arctic ground squirrels

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The wide-spread encroachment of canopy-forming shrubs into northern and alpine tundra communities is likely to alter many plant–animal interactions, with direct and indirect impacts on herbivore populations. Specifically, shrub encroachment may impact habitat quality for herbivores by changing predation risk as a result of reduced visibility. We investigated the association between visibility and growth of juvenile arctic ground squirrels *Urocitellus parryii* across an alpine tundra ecotone with varying shrub cover. Marked individuals were weighed throughout the period following emergence from natal burrows in early summer until just prior to hibernation. Both males and females showed a positive association between habitat-specific visibility and post-emergence growth rate. There was a positive relationship between post-emergence juvenile growth rate and pre-hibernation mass for females but not males. As shrubs increase, ground squirrel populations may be adversely affected by reductions in habitat-scale visibility.

Canopy forming shrubs are becoming more abundant in warming tundra ecosystems (Sturm et al. 2001, Myers-Smith et al. 2011, Elmendorf et al. 2012). Changes in shrub cover result in altered vegetation height and structure, and altered vegetation composition, which could affect habitat quality for many arctic species adapted to open landscapes (Sokolov et al. 2012). Changes in visibility associated with shrub encroachment may be particularly important drivers of change. Burrowing herbivorous mammals, such as arctic ground squirrels *Urocitellus parryii* are integral parts of tundra ecosystems, strongly influencing community composition and food webs via burrowing, foraging and as prey (Davidson et al. 2012, Wheeler and Hik 2013). As tundra habitats change in response to rapid warming, population responses of burrowing mammals could have cascading effects on local plant and animal communities (Ceballos et al. 2010, Davidson et al. 2012).

The conditions an individual experiences early in life may disproportionately influence its subsequent body mass and lifetime reproductive success (Lindström 1999). Body mass influences reproductive investment and survival (Murie and Boag 1984, Dobson and Kjelgaard 1985, Sauer and Slade 1987). For hibernators, greater mass prior to hibernation can increase the probability of over-wintering survival (Murie and Boag 1984, Lenihan and Vuren 1996, Schorr et al. 2009). During summer, juvenile arctic ground squirrels approximately triple in mass, with males gaining ~7 g and females gaining ~5 g per day (Buck and Barnes 1999). These high growth rates are likely related to the short period between emergence and hibernation which provides only a short opportunity for foraging (Kiell and Millar 1978). When mass gains or deficits incurred during the juvenile growth period continue throughout a lifetime, effects on reproductive success are likely (King et al. 1991, Neuhaus 2000). Thus, identifying the causes of poor juvenile growth will improve understanding of the processes regulating populations.

For arctic ground squirrels, boreal forest and dense shrub habitat appears to be lower quality than more open habitats. Greater survival, reproduction and density and lower instance of chronic stress are associated with more open habitats (Hik et al. 2001, Gillis et al. 2005a, Donker and Krebs 2012). Long-term burrow occupancy is also greater in high visibility areas (Karels and Boonstra 1999). We assess the associations between visibility and juvenile arctic ground squirrel post-emergence growth rate and juvenile pre-hibernation mass and evaluate competing explanations concerning predation risk and forage.

Visibility changes from altered vegetation stature could affect foraging efficiency via a number of effects on predator–prey interactions. Vegetation stature can affect predator identity (Cresswell and Quinn 2013), predation pressure (Laundre 2010) and ability of prey to detect predators. This combination of landscape features and areas of predator activity can create spatial variation in prey perception of risk, refered to as a 'landscape of fear' (van der Merwe and Brown 2008). Changes in real and percieved predation risk associated with visibility can influence the investment of time and

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energy in predator-sensitive behaviours and predator detection, and as such is a major determinant of habitat quality for many herbivores. High visibility can facilitate early predator detection, reduce the need for time and energy investment in predator sensitive behaviours (Arenz and Leger 1997, Bednekoff and Blumstein 2009) and thereby increase foraging efficiency (Mateo 2007). Juveniles may be especially responsive to factors affecting predation risk, due to their high vulnerability to predation (Carey and Moore 1986). Although herbivores often use high visibility to detect predators at a distance (Blumstein et al. 2006), they also use visual obstruction to seek refuge from predators (Wywialowski 1987, Sharpe and van Horne 1998, Hannon et al. 2006).

Changes in forage under shrub encroachment could also affect foraging efficiency. For species which forage directly on shrub such as browsing ungulates, shrub encroachment may improve foraging efficiency and a positive association between visibility and growth rate would be expected. For arctic ground squirrels, during the summer period when juveniles emerge, shrub itself does not appear to be important forage (Batzli and Sobaski 1980). However, if species composition or biomass associated with warming and shrub cover were associated with altered biomass of preferred forage species, juvenile growth rates and mass could be affected. If shrub habitat provided improved forage relative to tundra, growth rates should increase as visibility declined. If tundra habitat contained higher forage quality and quantity, we would expect growth rates to increase concomitantly with visibility.

To understand how shrub encroachment could affect ground squirrel population dynamics, we tested the importance of visibility on post-emergence juvenile growth and pre-hibernation mass. We posed two questions: 1) does visibility explain variation in growth rate and prehibernation mass across a shrub to tundra ecotone? 2) Do both sexes respond similarly to visibility? We then discuss the potential reasons for these associations with particular reference the relative support for predation-related versus forage-related hypotheses.

Material and methods

Study species

Arctic ground squirrels are a colonial rodent with a broad Holarctic distribution. They are found in northern North America and eastern Siberia across a relatively wide range of habitats (Wheeler and Hik 2013). Adult individuals can reach up to 1.1 kg in mass (Morrison and Galster 1975). Densities are highly variable; densities from 0.01 to 16 individuals per hectare have been recorded. They are prey to a diverse range of avian a terrestrial predators including grizzly bear, coyote, red fox, lynx, golden eagle, goshawk, great horned owl and gyrfalcon (Wheeler and Hik 2013).

Mark–recapture trapping

Arctic ground squirrels were studied in eight trapping grids across a gradient of habitats varying in density of canopy-forming shrubs in an alpine valley in the Ruby Range, southwest Yukon, (61°21′N, 138°27′W) in 2008 and 2009. Grids varied in shrub cover, from alpine tundra which had rare or occasional individual shrubs, rarely exceeding 20 cm in height, to dense shrub, which had almost contiguous shrub cover, with shrubs frequently reaching over 1 m in height. Shrub-tundra was intermediate to these, where taller shrubs occurred but canopy was not contiguous.

Capture–recapture trapping was conducted for all of eight 200×200 m (4 ha) grids using Tomahawk traps ($19 \times 6 \times 6$ inch) at 50 m spacing. All grids were separated by at least 400 m and juveniles were never captured in more than one grid. Trapping was conducted at each grid on at least five different days each month within a two-week period near the beginning of the month. Each trapping session lasted three hours; traps were checked hourly. Upon capture, juvenile squirrels were individually marked with tags and weighed, and sex was recorded. Techniques were approved by the Univ. of Alberta Animal Care Committee and followed the guidelines of the Canadian Council on Animal Care (CCAC 2003).

Growth rates and pre-hibernation masses

Growth rate and pre-hibernation mass were measured for individual male and female juvenile arctic ground squirrels in both 2008 and 2009. Growth rate was assessed for each individual ground squirrel for the period 1 July to 25 August. Coefficients from regressions of mass against dates, representing daily growth rate for an individual were compared between habitats. Juveniles emerge in early July, disperse 2–3 weeks after emergence (Byrom and Krebs 1999) and are thought to settle in their new habitats by mid-August (Green 1977, Gillis 2003), so these criteria should maximise the chances that growth rates represent those of individuals in their natal habitat. During this period, growth rates fit linear models well ($R^2 > 0.95$ in 82% of cases, minimum $R^2 = 0.82$) so linear models were applied throughout. In order to be included in the growth rate analysis, a minimum of four measurements of mass for an individual had to be made during this period, and at least one prior to 20 July. Sample size for juvenile growth rates was 25 females and 13 males and each data point represented a unique individual. To quantify pre-hibernation mass, the measurement nearest to 5 September (provided it fell within three days either side of this date) was used for each individual. Sample size for pre-hibernation mass was 14 females and 9 males, each data point represented a unique individual.

Habitat-scale visibility

Mean visibility to a distance of 25 m across the grid in which a juvenile was trapped was assessed using line of sight measurements. Line of sight was estimated on each site at twenty-five trapping locations within a 5×5 trapping grid with 50 m spacing between locations. The percentage of a 1×1 m board held vertically, with the bottom edge resting on the ground that was visible at a distance of 25 m at 20 cm above ground was estimated for each of four cardinal directions at each location. Observations were taken from 20 cm above the ground to reflect the approximate sight-line of an arctic ground squirrel in a vigilant posture.

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Statistical analysis

A general linear model was used to explore the effect of visibility and sex on growth rate. Within this model, we tested for a linear relationship between habitat visibility and post-emergence growth rate, and tested for a difference between sexes and also included an interaction between sex and habitat visibility. The effects of habitat visibility and sex on pre-hibernation mass were tested using an analogous general linear model with interaction term. The relationship between post-emergence growth rate and pre-hibernation mass was then assessed for males and females. Finally, to assess whether those individuals still present in the study sites prior to hibernation were a biased subset of those for which post-emergence mass was monitored (due to either condition dependent dispersal or condition dependent survival), the effect of presence in the pre-hibernation sample was added to visibility and habitat models of post-emergence mass. All statistical analyses were conducted in R (ver. 2.10.1).

Results

Growth rates were positively associated with habitat-scale visibility, with higher growth rates under higher habitat visibility ($F_{1,34} = 11.70$, $p = 0.002$, Fig. 1). Males had higher growth rates than females ($F_{1,32} = 23.70$, $p > 0.001$). The association between visibility and growth rate was similar magnitude for males and females, as demonstrated by no significant interactive effect of visibility and sex on growth rate ($F_{1,34} = 1.98$, $p = 0.163$).

Males had higher pre-hibernation mass than females (difference = 187.30 ± 93.27 g, $F_{1,18} = 9.65$, $p = 0.006$) but no significant effect of habitat visibility on pre-hibernation mass was observed ($F_{1,18} = 1.55$, $p = 0.228$) and there was no significant interactive effect of sex and visibility on pre-hibernation mass ($F_{1,18} = 0.77$, $p = 0.393$). Post-emergence growth rate was a good predictor of pre-hibernation mass for females ($F_{1,12} = 5.22$, $p = 0.041$, Fig. 2) but not for males ($F_{1,6} = 0.01$, $p = 0.929$, Fig. 2). There was no difference in post-emergence growth rates between juveniles present and those absent in the pre-hibernation sample after the effects of sex and habitat or visibility were taken in to account ($F_{1,33} = 0.332$, $p = 0.569$).

Discussion

We found variation in juvenile growth rates associated with visibility related to shrub cover, indicating that the consequences of increases in shrub cover could negatively affect juvenile growth rates. While associations between visibility and post-emergence juvenile growth were observed for both males and females, only females showed an association between post-emergence growth and pre-hibernation mass, suggesting that mass gain in males becomes less tied to habitat related factors as time processes through their first active season.

Our observation of reduced post-emergence juvenile growth rates under lower visibility indicates that encroachment of shrubs under warming could negatively affect a juveniles' ability to gain mass. The positive association between juvenile growth and visibility indicates that growth rates were higher in open habitats. According to our predictions, this suggests that either the structural architecture of shrub creates unfavourable foraging habitat, most likely by increasing predation risk or perception of risk, or vegetation communities associated with shrub contain less favourable forage for juvenile arctic ground squirrels. We suggest changes in the structural architecture of the vegetation are the most likely dominant factor causing these relationships.

In ground-dwelling sciurids, preference for foraging areas with elevated visibility has been demonstrated (Carey 1985).

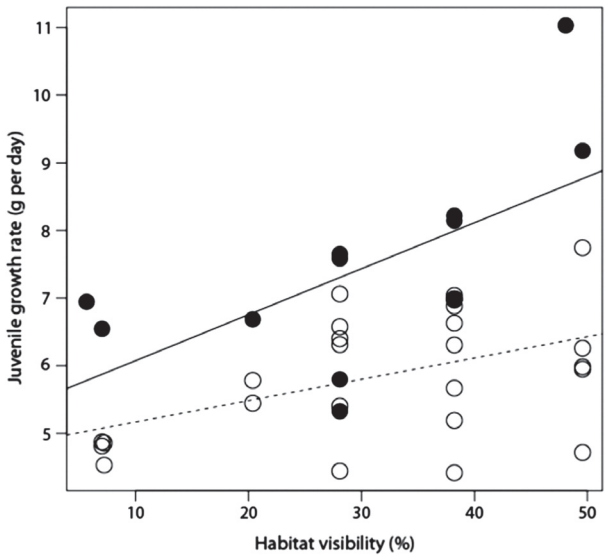


Figure 1. Effect of habitat type on juvenile arctic ground squirrel post-emergence growth rates between 1 July and 21 August. Open circles represent individual females and closed circles individual males. Regression lines are shown for females (broken) and males (solid).

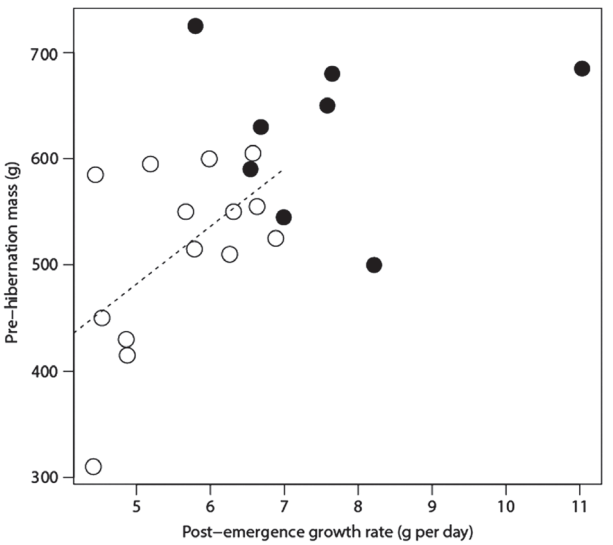


Figure 2. Relationship between arctic ground squirrel post-emergence juvenile growth (1 July to 21 August) and pre-hibernation mass (5 September ± 3 days). Open circles represent individual females and closed circles individual males. Regression lines are shown for females (broken).

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Chronic stress has been reported in arctic ground squirrels in low visibility habitats using haematological assessment of stress profiles (Hik et al. 2001) and indicates some combination of nutritional or predator induced stress. Behaviour of arctic ground squirrels at our site also indicates a lower foraging efficiency in shrub habitat (Wheeler 2012, Wheeler and Hik 2014). Lower foraging efficiency could occur if individuals devote more time to predator detection activities such as vigilance (Mateo 2007, Sharpe and van Horne 1998), or reduce time spent foraging, such as if individuals more frequently seek refuge in burrows due to 'false alarms' resulting from inferior detection ability or elevated response rates.

Low baseline faecal cortisol has been found in low visibility habitats in Belding's ground squirrel, associated with prolonged and more exaggerated predator sensitive responses (Mateo 2007). This low baseline cortisol has been linked to the ability to elicit a more pronounced acute cortisol response to threats (Mateo 2007). Similarly, lower baseline faecal cortisol has been found in arctic ground squirrels in shrub compared to tundra habitats in our population (Sheriff et al. 2012). These greater investments in predator sensitivity in visually obstructed habitats could contribute to reduced growth rates in visually obstructed shrubbier habitats via reduced foraging efficiency. Lower mass gain could be driven by a higher predation pressure, due to changes in predator community or activity associated with reduced visibility, or greater perception of fear associated with low visibility.

Forage might covary with visibility and affect juvenile foraging efficiency. Forage composition and quality affects juvenile growth and condition in many ground dwelling sciurid species (Bennett 1999, Woods and Armitage 2003). Arctic ground squirrels are generalist foragers, consuming broader varieties of plants than other arctic rodents (Batzli 1983). Due to higher protein content and greater digestibility, forbs (particularly legumes) are thought to provide better forage than grasses (Batzli and Sobaski 1980, McLean 1985). Foraging toward the end of the active season has not been extensively described, except for caching, where seed and rhizome acquisition is highly selective but dependant on local vegetation composition (Gillis et al. 2005b, Zazula et al. 2006). Transitions from tundra to shrub-dominated ecosystems can be associated with increased forb cover (Wookey et al. 2009, Pajunen et al. 2011) although responses are variable and highly contingent (Elmendorf et al. 2012, Villarreal et al. 2012), and such variation in forb cover with shrub cover has not been found in our site (Myers-Smith and Hik 2013). We find higher growth rates in open habitats than low visibility shrub habitats, which does not support any predictions of higher quality forage in shrub habitat, rather if forage was driving this relationship, forage quality must be higher in open tundra habitats. While there is little evidence to suggest this is the case in our study site, given many contingencies affect vegetation responses to warming, further understanding of arctic ground squirrel diet and habitat selection should be developed to understand how changing forage might affect this species under environmental change.

Although males and females responded similarly to habitat visibility early in the season as evidenced in trends with post-emergence growth rates, males had higher growth rates and higher mass than females and only females had pre-hibernation mass associated with post-emergence growth. Males showed no association between post-emergence growth and pre-hibernation mass. One possibility is these trends may reflect the combination of constraints on foraging early in the season which may be more influenced by parental and sibling behaviour, and greater compensatory growth in males once such constraints are reduced.

Males may have greater need to gain mass than females in their first year regardless of costs such as predation risk as a result of more intense selection on the mass of yearling males. Records of immergence timings from dates of last capture at a northerly location suggest juvenile females enter hibernation slightly earlier than males ($<90\%$ of juvenile females with date of last capture prior to 22 September, compared with 62.6% juvenile males (Buck and Barnes 1999). This suggests that males also require longer to accumulate mass than females.

Males experience extremely high costs of reproduction (Holmes 1977, Buck and Barnes 1999, 2003, Boonstra et al. 2001, Delehanty and Boonstra 2011). Given almost all yearling squirrels breed and that 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 Keenleys 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 and highly skewed. In contrast, mass is more likely to affect female reproduction in terms of available resources to invest in production and provisioning of young in a given year, which may represent a weaker selective force. These differences may result in weaker associations of male mass with habitat related variables once foraging is independent from the family group as the tradeoff between gaining mass and minimising predation risk may be more directed toward the former.

Our analysis indicates that juvenile growth rate is correlated with visibility and complements previous analyses demonstrating that more closed habitats are of lower quality for adults (Karels and Boonstra 1999, Gillis et al. 2005a, Donker and Krebs 2011, 2012). Our results suggest that shrub encroachment, has the potential to lead to negative effects on juvenile growth and mass. The effects of shrub cover on foraging conditions via forage quality and visibility may be important for the many species which rely on tundra species for forage and high visibility for predator detection and may result in altered communities under climate change.

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