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Forest or meadow: the consequences of habitat for the condition of female arctic ground squirrels (*Urocitellus parryii plesius*)

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Abstract: Body condition of animals influences the likelihood of surviving harsh environmental conditions, successfully reproducing, and resisting disease. The sum of these individual components of fitness, in turn, have consequences for the growth and persistence of wildlife populations. Here we compared the body mass and condition of adult female arctic ground squirrels (*Urocitellus parryii plesius* (Osgood, 1900)), an obligate hibernator, in source and sink habitats. We tested the hypothesis that adult females would be in poorer condition in the boreal forest than in adjacent meadows. We found that, during spring, postpartum females in forests weighed less (405 ± 7 vs. 437 ± 11 g; mean ± SE) and were in poorer condition (mean (±SE) residual of mass over structural size = −11.0 ± 10.2 vs. 20.5 ± 6.1 g) compared with females in meadow-source habitat. However, by the onset of entrance into hibernation in August, forest squirrels had reached parity with meadow squirrels and no difference was found in mass (519 ± 13 vs. 520 ± 15 g; mean ± SE) or condition (residual index = −0.01 ± 0.01 vs. 0.03 ± 0.01; mean ± SE). We suggest that for squirrels in formerly occupied boreal forests, (*i*) poor spring body condition decreased reproductive success and (*ii*) achieving compensatory growth, via increased foraging, comes at the costs of higher predation risk. These costs likely contributed to the recent local extinction of arctic ground squirrels in boreal forest habitat.

Key words: arctic ground squirrel, body condition, body mass, boreal forest, climate change, extirpation, foraging strategy, Kluane, predation risk, population collapse, source–sink, *Urocitellus parryii plesius*, vigilance.

Résumé : L'embonpoint des animaux influence la probabilité de survie dans des conditions ambiantes difficiles, le succès de reproduction et la résistance aux maladies. La somme de ces différentes composantes de l'aptitude a, quant à elle, des conséquences en ce qui concerne la croissance et la persistance des populations d'animaux sauvages. Nous comparons la masse corporelle et l'embonpoint de spermophiles arctiques (*Urocitellus parryii plesius* (Osgood, 1900)) femelles adultes, une espèce hibernante inféodée, dans des habitats sources et puits. Nous vérifions l'hypothèse selon laquelle les femelles adultes présenteraient un moins bon embonpoint dans la forêt boréale que dans les baissières adjacentes. Nous avons constaté que, au printemps, les femelles post-partum dans les forêts présentaient une masse (405 ± 7 contre 437 ± 11 g; moyenne ± ET) et un embonpoint (résidu moyenne (±ET) de la masse sur la taille structurale = −11,0 ± 10,2 contre 20,5 ± 6,1 g) inférieurs à ceux des femelles dans les habitats sources de baissière. Cependant, au début de l'entrée en hibernation en août, les spermophiles des forêts avaient atteint la parité avec les spermophiles des baissières et aucune différence de masse (519 ± 13 contre 520 ± 15 g; moyenne ± ET), ni d'embonpoint n'était observée (indice résiduel = −0,01 ± 0,01 contre 0,03 ± 0,01; moyenne ± ET). Nous proposons que, pour les spermophiles dans des forêts boréales occupées antérieurement, (*i*) le faible embonpoint printanier réduisait le succès de reproduction et (*ii*) la compensation de la croissance par un approvisionnement accru vient au coût d'un risque de prédation accru. Ce coût a probablement contribué à la disparition locale récente de spermophiles arctiques dans des habitats de forêt boréale. [Traduit par la Rédaction]

Mots-clés : spermophile arctique, embonpoint, masse corporelle, forêt boréale, changement climatique, disparition locale, stratégie d'approvisionnement, Kluane, risque de prédation, effondrement de populations, source–puits, *Urocitellus parryii plesius*, vigilance.

Introduction

For many mammals, body mass and body condition are important determinants of overwinter survival (Festa-Bianchet et al. 1997), reproductive success (Guinet et al. 1998), and susceptibility to disease (Beldomenico and Begon 2010). A positive association between stored energy reserves and overwinter survivorship in hibernating mammals has been documented extensively (e.g., Armitage et al. 1976; Murie and Boag 1984; Neuhaus 2000). Individuals that weigh more upon entrance into and emergence from hibernation reproduce more frequently and have larger and more successful litters (Rieger 1996; Millesi et al. 1999).

Habitat quality may determine the body condition of individuals who reside in different habitat patches, affecting habitat-specific demographic rates that define population "sources" and "sinks" (Pulliam 1988). In poor-quality habitat, local yearly recruitment is not related to reproduction or survival rates of patch residents; these "sink" habitats are net importers and extinction would be inevitable without sufficient immigration from sources (Dias 1996). Source–sink theory seeks to explain the existence of space-specific demography in connected wildlife populations.

In this study, we compare spring and autumn body mass and body condition of adult female arctic ground squirrels (*Urocitellus parryii plesius* (Osgood, 1900); AGS) in source and sink habitats in the boreal region of southwestern Yukon, between 2000 and 2009. Within this region, AGS occupy three main habitats: boreal forest, low-elevation meadows (herein also referred to simply as low meadows), and alpine tundra. Populations in the boreal forest historically

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fluctuated with the 9- to 10-year snowshoe hare (*Lepus americanus* Erxleben, 1777) population cycle due to prey switching of specialist and generalist predators during the years when hares became scarce (Boutin et al. 1995). However, following the 1998 snowshoe hare peak in the Kluane region of southwestern Yukon, boreal forest populations failed to recover and since 2000 have remained near zero (Werner et al. 2015). In contrast to this dramatic disappearance, AGS in nearby low- and high-elevation meadows are common (Green 1977; Gillis et al. 2005; Werner et al. 2015) and populations appear stable in these meadow habitats (Donker and Krebs 2011). We evaluate two broad hypotheses to explain the observed habitat-specific dynamics:

1. Source and sink habitats differ in feeding conditions and that high overwinter mortality generates sink demography. From this we predict that AGS in source habitats are in better body condition when entering hibernation and soon after emerging the following spring compared with AGS in sink habitats.

2. Source–sink dynamics are driven primarily by active season mortality, possibly predation. From this we predict no significant differences in body condition of AGS from source and sink habitats when individuals enter hibernation and after emergence the next spring.

Materials and methods

Study species

AGS are the largest and most northerly distributed of all ground squirrels in North America (Naughton 2012), where they occupy arctic tundra, alpine areas, and the montane boreal forest of northwestern Canada and Alaska (Nadler and Hoffmann 1977; Naughton 2012). They are active for only 3–5 months per year and the majority of their life history comprises a 7–9 month hibernation period lasting from as early as mid-August to as late as late May (Carl 1971; McLean and Towns 1981). Females breed within days of spring emergence (mid-April) and produce a single litter ~25 days later (mid-May) (Green 1977; Lacey et al. 1997; Karels et al. 2000; Sheriff et al. 2010). Juveniles are weaned and emerge from their natal burrow in mid- to late June. Nearly all males disperse, whereas most females settle within their natal home range (mean dispersal distance of males and females was 515 and 120 m, respectively; Byrom and Krebs 1999). Adult females are at their lowest body mass at emergence and, in arctic tundra, mass does not increase for the first month (Buck and Barnes 1999a; Sheriff et al. 2013); however, in southwestern Yukon, adult females are reported to accrue mass immediately after emerging from hibernation and continue to do so through parturition (McLean and Towns 1981).

Study area

AGS were studied in the Kluane region of the Yukon Territory, Canada, in two valley bottom habitats: boreal forest (~900 m above sea level (asl)) and low meadow (~800 m asl). In the boreal forest, data were collected from 2000 to 2009 on two live-trapping grids (~900 m asl; 61°00′38″N, 138°11′31″W and 60°55′53″N, 137°58′25″W) located ~20 km from each other. These grids were dominated by a white spruce (*Picea glauca* (Moench) Voss) forest, small clearings, and willow (genus *Salix* L.) thickets with occasional aspen (genus *Populus* L.) stands (described by Krebs et al. 2001 and Gillis et al. 2005). In the low meadow (~10 ha in size), data were collected from 2008 to 2009 on one grid dominated by grasses and surrounded by boreal forest (described by Green 1977; Donker and Krebs 2011). On the boreal forest grids, AGS population density was 0.38 ± 0.13 squirrels/ha (all age and sex classes combined) in 2000 and declined to extirpation by 2009; in the low meadows, AGS density was stable between 2008 and 2009 at 1.25 ± 0.22 squirrels/ha (Donker and Krebs 2011).

Trapping and handling

In the boreal forest, AGS were captured on 10 ha grids with traps spaced 30 m apart in a 10 × 10 pattern, with traps placed at alternate grid stakes. The number of unique adult females captured over the entire 10-year period was 45 and 36 during spring and autumn, respectively. At the low-meadow site, squirrels were captured on a 10 ha grid with traps spaced 50 m apart in a 5 × 10 pattern. The number of unique females captured during spring and autumn was 24 and 17. These numbers are a reflection of the low population densities at both sites (see below).

Each year, trapping was conducted for four consecutive days between 21 and 29 May, from the hours of 0700 to 1100 (except in 2009 where trapping at the low-meadow site was extended to five consecutive days in response to cold temperatures and low capture success). Autumn trapping was conducted 1–11 August and consisted of between two and four consecutive days of trapping. We used Tomahawk live traps (14 cm × 14 cm × 40 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with peanut butter. Upon capture, adult females were transferred to a mesh bag, tagged with Monel No. 1005-1 tags in both ears (National Band and Tag Co., Newport, Kentucky, USA), weighed with a Pesola spring scale (accurate to ±5 g), sexed, and skull width measured (±0.5 mm). This research was approved by The University of British Columbia Animal Care Committee in accordance with the guidelines of the Canadian Council on Animal Care.

Statistical analyses

We used a two-way ANOVA to test for the main effects of season and habitat, as well as the interaction of season and habitat on mass patterns at parturition and prior to entrance into hibernation. To determine the body condition of adult females, we obtained the residuals of body mass (g) regressed on zygomatic arch width (a reliable estimate of skeletal size; Dobson 1992; Dobson and Michener 1995; Karels 2000; Schulte-Hostedde et al. 2005) with simple linear regression using ordinary least squares. Jakob et al. 1996 and Schulte-Hostedde et al. (2005) assessed techniques for determining body condition and report that this method performs best. We then used this metric of body condition in a second model to investigate the effects of habitat and season on adult female AGS body condition. Differences between mean residuals were tested using a two-sample t test. All statistical analyses were calculated using program JMP version 4.0 (SAS Institute, Inc., Cary, North Carolina, USA). Prior to analysis, data for mass and size were assessed for normality and homogeneity of variance (Shapiro–Wilk's test) and subsequently log-transformed. No significant interannual differences in mass or condition were found among years within each habitat type and data were pooled. Furthermore, to explore the seasonal relationships between body mass and condition, we obtained r^2 values for regressions of the residual index on body mass. All data are presented as means (back-transformed) ± SE.

Results

Body mass and size

We found a significant main effect of both season ($F_{[1,121]} = 140.564$, $P < 0.001$) and habitat ($F_{[1,121]} = 9.814$, $P = 0.002$) on the mass of adult females. There was also a significant interaction between the effects of season and habitat type on the mean mass of adult females ($F_{[1,121]} = 4.859$, $P = 0.029$; Fig. 1). Overall, females increased their body mass from late May to early August by approximately 25%. In spring, females were 8% heavier in the low meadow (437 ± 11 g) compared with those in the boreal forest (405 ± 7 g); by autumn, body mass was comparable (520 ± 15 g (low meadow) compared with 519 ± 13 g (boreal forest)).

We found a significant main effect for season on structural size ($F_{[1,121]} = 13.360$, $P < 0.001$) and a slight main effect of habitat on size ($F_{[1,121]} = 2.914$, $P = 0.09$). No interaction effect of habitat and season

Fig. 1. Spring and autumn body mass (mean ± 95% confidence intervals) of adult female arctic ground squirrels (*Urocitellus parryii plesius*) in boreal forest and low-elevation meadows (low meadow) of the Kluane region, southwestern Yukon. Spring—low meadow: 437 g, *n* = 24; boreal forest: 405 g, *n* = 45. Autumn—low meadow: 520 g, *n* = 17; boreal forest: 519 g, *n* = 36. Two-sample *t* test: $t_{[55]} = 2.40$, $P = 0.02$.
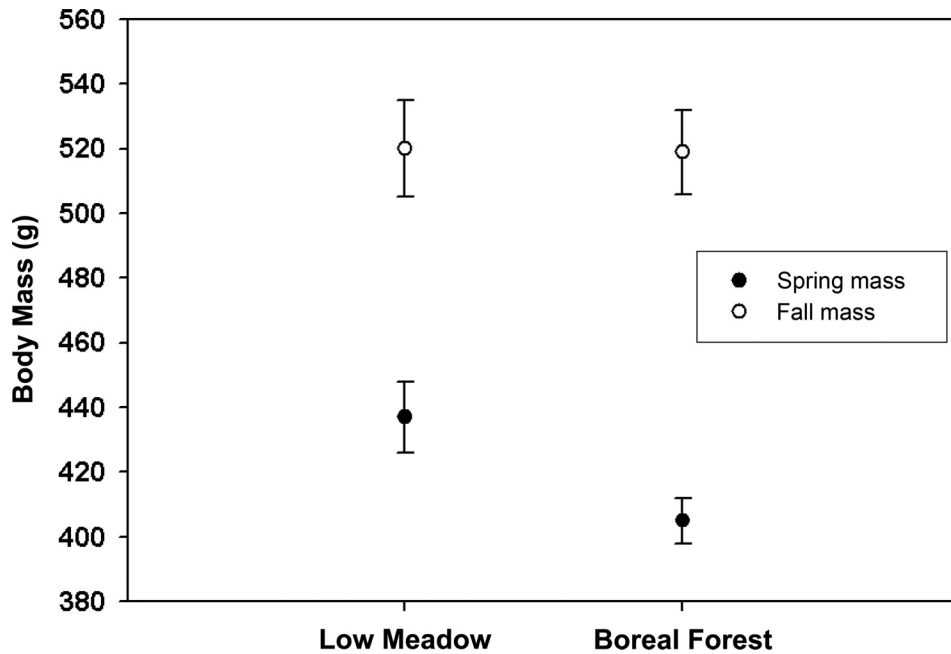
were detected ($F_{[1,121]} = 0.011$, $P = 0.9$). Overall, adult females were ~3% larger during autumn than during early spring (mean zygomatic arch breadth; spring—low meadow: 33.09 ± 0.23 mm; boreal forest: 33.54 ± 0.32 mm; autumn—low meadow: 34.12 ± 0.22 mm; boreal forest: 34.63 ± 0.21 mm).

Body condition

Body condition of adult females was estimated as the residuals in a regression of seasonal body mass on structural size (zygomatic arch breadth). The first model using spring body mass regressed on skull width was significant ($y = 11.05x + 26.23$; $r^2 = 0.11$, $n = 69$, $F_{[1,68]} = 6.57$, $P = 0.01$). The second regression model of autumn body mass on skull width was also significant ($y = 2.45x - 1.06$; $r^2 = 0.38$, $n = 53$, $F_{[1,51]} = 31.6$, $P < 0.001$). These results indicate that size explains more of the variation in mass during autumn than during spring (~3.5 times). The residuals from these models are, by definition, independent of size (confirmed by inspection of residual plots). We then compared the mean values of these residuals between habitats and found that female AGS who reside in the boreal forest had lower spring body condition (mean residual = −11.0 ± 10.2 g) compared to those in low meadows (mean residual = 20.5 ± 6.1 g; Fig. 2) ($t_{[68]} = 2.47$, $P = 0.01$). In autumn, boreal forest females also had lower, but not significantly different, body condition (mean residual = −0.01 ± 0.01 g; Fig. 3) than low meadow females (mean residual = 0.03 ± 0.01 g) ($t_{[52]} = 2.76$, $P = 0.8$). Winter conditions during 2007–2008 and 2008–2009 (the period during which low meadow data were collected) were characterized by relatively little snowfall and cold temperatures (Fig. 4). Any yearly biases in spring mass caused by poor hibernation conditions during this time will result in an underestimate of reported differences between habitats.

We found that the relationship between mass and condition changed with season. During spring, body mass was a very good predictor of body condition in both habitats (boreal forest condition regressed on mass: $r^2 = 0.87$; low meadow condition regressed on mass: $r^2 = 0.97$, Table 1), but the strength of these correlations decreased by onset of autumn (boreal forest condition regressed on mass: $r^2 = 0.58$; low meadow condition regressed on mass: $r^2 = 0.66$, Table 1). Where spring data on condition of adult female AGS

are lacking measures of mass, regardless of structural size, may therefore serve as a useful surrogate.

Discussion

Despite wide recognition linking patterns of seasonal mass gain and body condition with survival (Armitage 1981; Festa-Bianchet et al. 1997; Cook et al. 2004), reproduction (Clutton-Brock et al. 1986; Barash 1989; Guinet et al. 1998), and population growth (Kilgore and Armitage 1978; Ozgul et al. 2010), and despite the acknowledgement of habitat-specific demography in AGS (Gillis et al. 2005; Donker and Krebs 2011), this constitutes the first comparison of mass and condition between adjacent habitat types. Our results support our hypothesis that adult female AGS in sink habitat (boreal forest) weigh less (Fig. 1) and are in worse condition (Fig. 2) in spring compared with those in source low meadows. However, these differences did not persist into autumn and both boreal forest and low meadow AGS were of similar mass and condition just prior to entering hibernation.

What causes differences in spring body mass and condition?

We identify three plausible, nonexclusive, causes for these inequalities in mass and condition. First, heightened mass gain may be a direct benefit accrued to females who do not successfully reproduce. Unsuccessful females avoid the energetic expenditure associated with lactation and rearing of young and may begin mass gain far earlier in the season, giving them a substantial advantage as far as mass gain is concerned. However, we view this explanation as unlikely because these nonreproductive females should be heavier by late May as a consequence of these energetic savings accrued during the previous month.

Secondly, this may be a consequence of environmental conditions during the early spring. At this initial stage of the vegetative growing season, forbs have not yet emerged and AGS must forage on woody browse, seeds, and dead grass from the previous summer. Persistent snow cover will directly interfere with a squirrel's ability to encounter these food items, while further delaying plant phenology and, thus, the quantity of available forage during May.
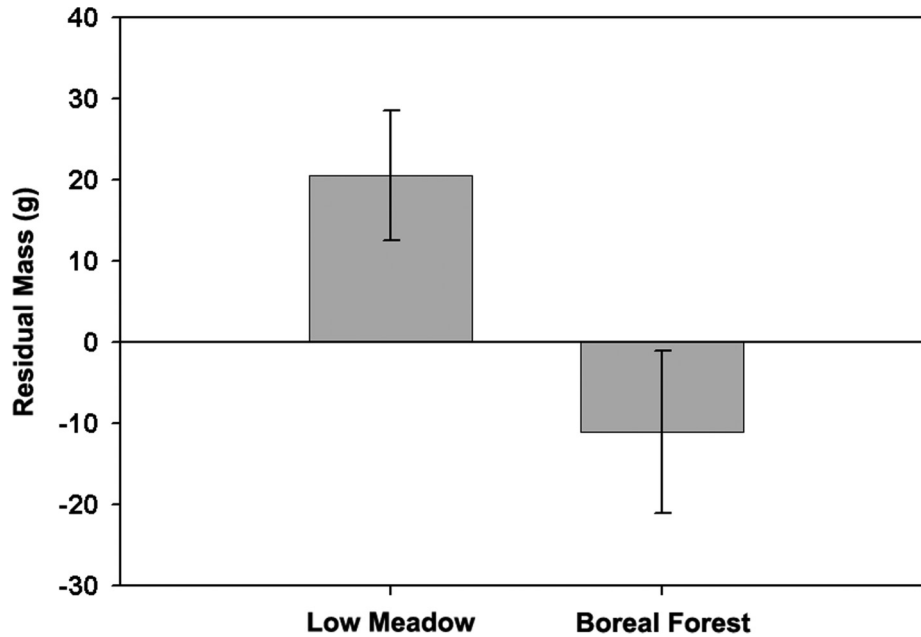
Fig. 2. Spring body condition index of adult female arctic ground squirrels (*Urocitellus parryii plesius*) in two contrasting, low-elevation (~800 m) habitats (i.e., boreal forest and low-elevation meadows (low meadow)) of the Kluane region, southwestern Yukon. Bars represent 1 SE. Low meadow: 20.5 g, *n* = 24; boreal forest: −11.0 g, *n* = 45. Two-sample *t* test: $t_{[68]}$ = 2.47, *P* = 0.01.

Fig. 3. Autumn body condition index of adult female arctic ground squirrels (*Urocitellus parryii plesius*) in two contrasting, low-elevation (~800 m) habitats (i.e., boreal forest and low-elevation meadows (low meadows)) of the Kluane region, southwestern Yukon. Bars represent 1 SE. Low meadow: 0.03 g, *n* = 17; boreal forest: −0.01 g, *n* = 36. Two-sample *t* test: $t_{[52]}$ = 2.76, *P* = 0.8.
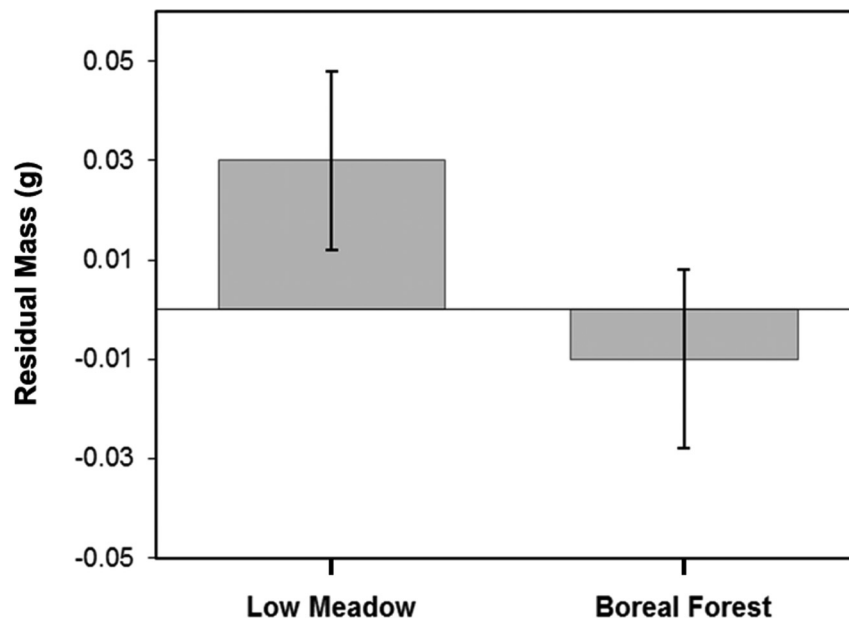
Habitat-specific mass patterns may therefore be governed by habitat-specific foraging opportunities.

Lastly, differences in mass and condition may be a reflection of the overwintering environment. We suggest that boreal forest squirrels may face greater physiological demands during hibernation that result in poor spring body condition. In the boreal forest, females select small open areas as hibernation sites, presumably because snow accumulation and soil temperatures are greater (Karels 2000). Because female AGS are sedentary (Byrom and Krebs 1999) and openings make up only >25% of the area in the boreal forest, differences in the availability of optimal hibernacula between boreal forest and low meadow habitats may contribute to

differences in spring body condition observed between habitats (but see Buck and Barnes 1999*b*). We do not directly test these competing hypotheses and, although they warrant further scrutiny, we emphasize that contemporary density of squirrels in boreal forest habitats (~0 individuals/ha) does not permit such study.

What are the consequences for habitat-specific body mass and condition?

Body mass

Adult female AGS living in the boreal forest weighed significantly less, during spring, than AGS that lived in nearby low

Fig. 4. Difference in mean monthly temperature (shaded) and mean precipitation (open) from long-term averages (1980–2014). Data from the Haines Junction Airport Meteorological Station, Environment Canada. Mass data collected during 2008–2009 from low-elevation meadow habitat are represented by relatively low temperatures and snow cover.
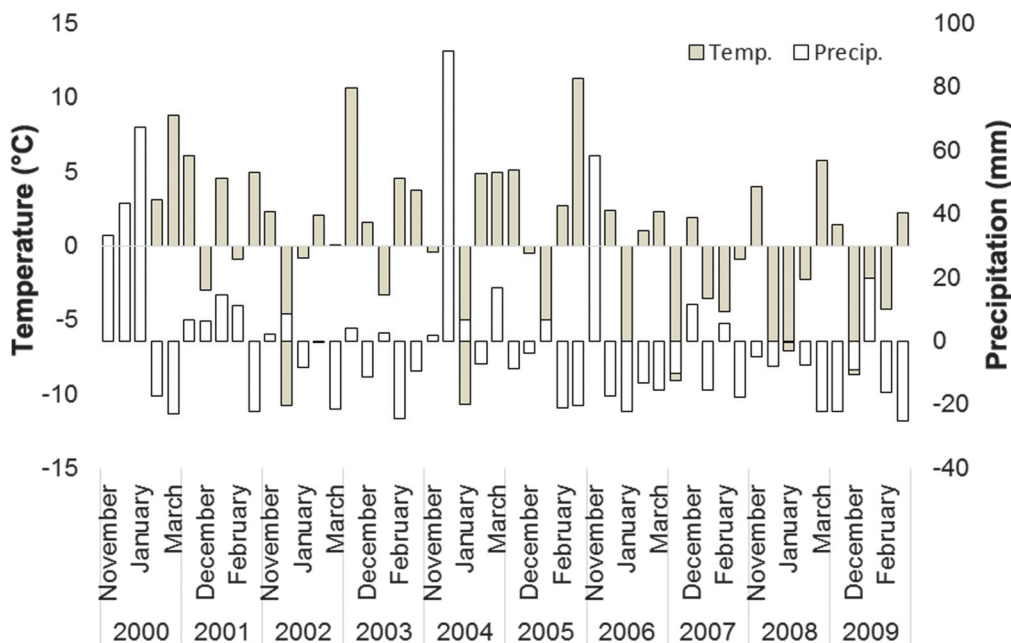

Table 1. Coefficient of determination for seasonal linear regressions of body condition (residual index) over log body mass (g) of adult female arctic ground squirrels (*Urocitellus parryii plesius*) in low-elevation meadow (low meadow) and boreal forest habitats during May and August, 2000–2009, in southwestern Yukon.

	Spring			Autumn		
	r^2	n	Linear regression	r^2	n	Linear regression
Boreal forest	0.87	45	$y = 16.33x - 42.619$*	0.58	36	$y = 8.8527x - 23.747$**
Low meadow	0.97	24	$y = 14.337x - 37.064$*	0.66	17	$y = 8.8722x - 23.715$
Combined	0.86	69	$y = 15.764x - 41.024$*	0.62	53	$y = 9.0041x - 24.125$

Note: *, $P < 0.001$; **, $P < 0.01$.

meadows. However, by the onset of entrance into hibernation, females in both habitats weighed the same (Fig. 1). Demographic implications of low spring mass for female AGS are low reproductive success and small litter sizes, but also increased overwinter survival because lighter individuals are unlikely to bear the energetic costs of reproduction (Rieger 1996; Millesi et al. 1999; Karels et al. 2000). For example, female Columbian ground squirrels (*Spermophilus columbianus* (Ord, 1815) = *Urocitellus columbianus* (Ord, 1815)) that are lighter during spring will often not reproduce, but experience greater subsequent overwinter survival compared with heavier females that successfully raise litters (Neuhaus 2000). Similarly, Donker and Krebs (2012) found that AGS overwinter survival was higher, but reproduction was lower, in the boreal forest habitat than in the low meadow habitat.

Body condition

We also found that adult female AGS in boreal forest (sink) habitat were in worse condition, during spring, than those in nearby low meadows. Differences in the body condition of females can have pronounced population-level consequences directly, via reduced survivorship, and indirectly, via reduced reproduction (Dobson and Michener 1995). Studies of Richardson's ground squirrels (*Urocitellus richardsonii* (Sabine, 1822)) (Dobson et al. 1999) and Columbian ground squirrels (Skibiel et al. 2009) found that mothers in worse body condition produced fewer young and that female offspring from these smaller litters were less likely to survive their first winter.

Poor body condition may also increase an individual's vulnerability to predation, particularly if the focal species is a secondary prey item to a dominant predator. For red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)) in Idaho, USA, a system where snowshoe hares were the primary prey species, those in poor condition were more intensely predated (Wirsing et al. 2002). In the Yukon boreal forest, AGS are a secondary prey with snowshoe hares again being the primary prey. In this system, squirrels who are in poor condition also experience higher predation (Donker and Krebs 2011).

It is instructive to note that during spring (and regardless of habitat), body mass correlated highly with body condition (r^2 = 0.87–0.97; Table 1), such that comparisons of mass alone would have served well for this study. The strong redundancy observed during spring between mass and condition weakens as individuals undergo variable rates of prehibernation fattening (August: r^2 = 0.58–0.66); we therefore caution against the use of similar substitutions during autumn.

Mass gain

A fundamental challenge for prey is to achieve a minimum energy balance (in the case of AGS and all hibernators, it must be positive over the course of an active season), while minimizing predator encounters. This conflict is central to an understanding of individual behaviour (Lima and Dill 1990) and habitat-specific distributions of wild populations (Brown 1988). Food acquisition and escape are often considered to be trade-offs, expressed by the

opposing activities of foraging and vigilance. The key question here is what costs are incurred by boreal forest females who maintain a greater active-season growth rate to achieve similar prehibernation mass compared with those females inhabiting low meadow habitats.

As AGS "must survive hibernation" if they are to breed, we should expect them to tolerate higher predation risk if it will help minimize overwinter mortality (Karels et al. 2000) (sensu the predation–starvation hypothesis; McNamara and Houston 1990). In a study by Karels et al. (2000), predation risk was manipulated through large (~1 km²) exclosures and the reproductive behaviour of female AGS was measured. The lower reproductive success on control grids and superior weaning rates in predator exclosures (Karels et al. 2000) point to the sublethal effects of mammalian predators (Preisser et al. 2005) in the boreal forest system. Moreover, despite predator exclusion improving female body condition and subsequent reproduction, the authors found no effects of predator exclusion on overwinter survival. In light of habitat parity in autumn mass (our study) and the lack of evidence linking more food and fewer predators to better overwinter survival in the boreal forest (Hubbs and Boonstra 1997; Karels et al. 2000), adult mass gain appears strongly compensatory. Overwinter survival "at all costs" is likely an essential life-history strategy for this and other hibernating species.

Negative population growth (Donker and Krebs 2011) and low colony occupancy (~4%; Werner et al. 2015) are contemporary features of AGS populations in the boreal forest of southwestern Yukon. We hypothesize that being in poor spring body condition may influence reproduction and active-season survival. AGS under heightened pressure to achieve sufficient fat and muscle reserves (Boonstra et al. 2014) to survive a long hibernation period likely forego strategies that maximize short-term survival (vigilance) for behaviours intended to ensure successful hibernation (foraging). The prioritization of foraging over safety could be expressed in two ways. First, adult females will devote more of their aboveground activities to foraging (presumably at a cost to vigilance behaviour). Second, vigilance is maintained while total time spent above ground is lengthened—either as the fraction of daily activity or by delaying hibernation. These predictions can be tested by obtaining activity budgets and dates of late-summer immergence. There are currently insufficient numbers of AGS in the boreal forests of this region to test this foraging–vigilance hypothesis.

In summary, we found that females had lower spring mass and were in poorer body condition in the boreal forest compared with those in the low meadow; these circumstances are associated with low reproductive success and reduced summer survival (Gillis et al. 2005; Donker and Krebs 2011). However, boreal forest females exhibited compensatory mass gain. We submit that females with elevated rates of mass gain must prioritize long-term energy storage over short-term safety and that this shift further exacerbates predation risk in the boreal forest (Hik et al. 2001). Alternatively, boreal forest females may achieve greater mass gain because poor reproductive success saves energy normally required for gestation and lactation. Furthermore, in northern ecosystems, global warming is predicted to intensify this trade-off, as the role of predation in regulating small herbivores increases (Legagneux et al. 2014). These factors may contribute, in concert, to maintaining the source–sink relationship between boreal forest and low meadow habitats and also to the recent population collapses of AGS (Werner et al. 2015) in the Kluane region.

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