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The impact of snow accumulation on a heath spider community in a sub-Arctic landscape

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Abstract Patterns of snow cover across the Arctic are expected to change as a result of shrub encroachment and climate change. As snow cover impacts both the subnivean environment and the date of spring melt, these changes could impact Arctic food webs by altering the phenology and survival of overwintering arthropods, such as spiders (Araneae). In this field study, we used snow fences to increase snow cover across a series of large (375 m^2) heath tundra plots and examined the effects on the local spider community during the following growing season. Fences increased snow cover and delayed melt on the treatment plots, paralleling the conditions of nearby shrub sites. Frequent sampling over the season revealed that increased snow cover did not affect spider abundance across different genera nor did it affect overall community composition.

Further, our snow treatment did not affect the dates when plots achieved seasonal catch milestones (25, 50, 75 % of total seasonal catch). Increased winter snow cover did, however, produce higher body masses in adults and juveniles of the dominant species *Pardosa lapponica* (Lycosidae), beginning immediately after snow melt until midway through the growing season. In addition, ovary/oocyte mass of mature *P. lapponica* females was significantly higher on treatment plots during the peak reproductive period. This is the first experimental manipulation study to report a significant effect of landscape-level changes to winter snow cover on the biomass of an Arctic macroarthropod.

Dedicated to the memory of Robert L. Jefferies for his lifetime of excellence in teaching and research.

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Introduction

Over the past half century, deciduous shrubs (particularly *Betula, Salix,* and *Aldus* species) have expanded substantially throughout the sub-Arctic tundra and boreal forest-tundra ecotone, with an average increase in landscape coverage of approximately 5–15 % (Sturm et al. 2001a; Tape et al. 2006; Hudson and Henry 2009; Olthof and Pouliot 2009). Experimental work suggests that this has been driven by temperature-induced shifts in litter decomposition (Cornelissen et al. 2007) and mineralization (Dormann and Woodin 2002; Rinnan et al. 2007). Increased shrub density may also facilitate intraspecific recruitment and growth by increasing winter nutrient release (Sturm et al. 2001b, 2005), allowing shrub coverage to continue to increase even without associated increases in air temperature.

The encroachment of shrubs on the tundra generally increases local winter snow pack, as the comparatively tall shrubs act as wind breaks, collecting snow blown from exposed ridges and reducing the wind-driven sublimation of snow directly upwind/downwind of shrub stems. This effect may increase winter snow depth by 20–100 % relative to shrub-free areas receiving similar levels of precipitation (Liston et al. 2002; Pomeroy et al. 2006).

The impact of climate change on snow cover in the Arctic is less clear. While the general trend has been a marginal decrease in winter snow depth (Liston and Hiemstra 2011), there is strong regional variability and some areas of northern Canada, Alaska, and Russia have experienced long-term increases in snow cover despite warmer temperatures (Serreze et al. 2000; Hinzman et al. 2005).

Due to their sensitivity to snow cover and the timing of snow melt (Strathdee and Bale 1998; Danks 2004; Dollery et al. 2006; Høye and Forchhammer 2008), Arctic arthropods are likely to be affected by any significant changes to winter snow depth brought on by shrub encroachment, climate change, or a combination of both. Arctic spiders (Araneae), in particular, may be severely impacted by changes to winter snow pack. These spiders require multiple growing seasons to reach maturity and tend to overwinter as adults or juveniles instead of eggs (Gertsch 1979; Danks 1999). They are cold-tolerant but many produce antifreeze proteins (Duman et al. 2004) and can be active during the winter (Hågvar 2010; Hågvar and Hågvar 2011). Although the functional significance of spiders in the Arctic is poorly known, they are highly abundant on the tundra and are frequently preyed upon by tundra birds during the breeding season (Hussell 1972; Baker 1977; Seastedt and MacLean 1979; McKinnon et al. 2012; G Legault and RL Jefferies personal observations). Further, they emerge early in the spring, reaching high abundance well before other macroarthropod taxa (Høye and Forchhammer 2008; G Legault unpublished data), and so may serve as primary forage for early-arriving bird species (e.g., Eeva et al. 2000). Since many Arctic birds are not capital breeders and depend on early-season forage to ensure survival and reproductive success (Klaassen et al. 2001), if spider abundance or phenology patterns were to shift due to changes to winter snow cover, then there could be serious consequences for many avian species (Pearce-Higgins et al. 2005 ; Meltofte et al. 2007; Tulp and Schekkerman 2008; McKinnon et al. 2012).

In this study, we examined how changes to winter snow cover and spring melt date affected patterns of abundance, community structure, phenology, body mass, and reproductive potential of a spider community in a sub-Arctic landscape. To do so, we manipulated winter snow depth using snow fences, a technique that is common to studies looking to simulate shrub encroachment (see Wipf and Rixen 2010), and studied their effects on the local spider communities the following spring.

Methods

Study site

The experiment was conducted between November 2009 and August 2010, approximately 23 km east of the town of Churchill, Manitoba (N58.73527, W93.80790), in a sub-Arctic zone on the northwest rim of the Hudson Bay Lowlands. We focused on heath tundra systems, which make up between 10 and 20 % of the vegetated area in the low Arctic (Walker et al. 2005). Sampling efforts in previous years indicated that heath contained a higher prevalence of terrestrial arthropods and that they were frequent foraging sites for breeding birds, such as Hudsonian Godwits (Limosa haemastica), American Golden-Plovers (Pluvialis dominica), Whimbrels (Numenius phaeopus), and Short-billed Dowitchers (Limnodromus griseus) (G Legault and RL Jefferies, unpublished data). Further, the dominant tall, deciduous shrub in the area (Betula glandulosa) is likely to expand onto or near to heath sites in the future (Myers-Smith et al. 2011).

The heath sites chosen for the experiment were on slightly elevated ridges (<1 m higher than the surrounding vegetation) adjacent to the areas of high deciduous shrub coverage. Winter snow cover is typically low on the sites (between 0 and 30 cm of snow in late March) and they are usually the first vegetated areas to melt out in the spring (late May to early June). Following melt, there is no standing water, though the acidic soil remains moist until midsummer, when water becomes limiting. Active layer depth is highly variable, but is rarely less than 10 cm or more than 35 cm ($\bar{x}$ = 20.03 cm, σ^2 = 10.37). Above the soil layer is a loose mat of vegetation, 10–20 cm thick, consisting chiefly of lichen interspersed with ericaceous shrubs and a small number of low-growing deciduous shrubs.

Snow treatment and small-scale trench experiment

At the beginning of winter (November 2009), 12 heath tundra sites within a 2 km radius were selected based on their similar vegetation and elevation. Six of these sites were randomly assigned the snow treatment, while the other 6 became control sites that were left untouched until sampling began in the spring. For each treatment plot, a snow fence constructed of a single layer of 50/50 circular mesh (15 m long and 1.5 m tall—consistent with the height of deciduous shrubs in the area) was positioned in the

center of the plot, perpendicular to the prevailing wind direction (NW). Plots were then left undisturbed until the spring, except for occasional fence maintenance and a formal assessment of winter snow depth approximately 1 month prior to local snow melt (control and treatment plots),

Site surveys during the winter indicated that each fence affected snow depth both in front of and behind the fence, with fences affecting a minimum area of approximately 375 m^2 (25 m × 15 m). To standardize plot size and prevent contamination by terrestrial arthropods from the surrounding environment, we fixed plot perimeters (control and treatment) following snow melt to 25 m × 15 m rectangles by digging trenches (30 cm deep and 20 cm across) around each plot. In most cases, the bottoms of these trenches were filled with water from melted permafrost for most of the summer season, which we took to be an effective barrier to the dispersal of ground-dwelling arthropods between plots. Limiting dispersal in this fashion meant that any observed differences in abundance, mass, or community structure between plots could be attributed to our snow treatment rather than factors outside of our plots.

To test the efficacy of the trenches at excluding terrestrial arthropods, we performed a small-scale trench experiment on two nearby heath tundra sites. Pitfall traps were placed in the ground and were subjected to three different trench treatments. "Open" traps were not surrounded by trenches, "tight" traps were surrounded by trenches with no space between the trench and the trap, and "wide" traps were surrounded by trenches with 50 cm of vegetation between the trap and each side of the trench ($n = 10$ for each trench treatment). We recorded the number of spiders caught in each of the traps over a 1-day and 5-day period.

Arthropod sampling

Sampling began in each experimental plot a day following spring melt, which we defined as the first day of the year when the entire 25 m × 15 m area of a plot was snow-free. In cases where snow melt was not uniform within a plot, snow-free areas were typically frozen and free of arthropod activity prior to complete snow melt. For the control plots, we observed a small number of spiders active on plots following melt, but we were not able to catch any using our pitfall trapping method until 2 weeks after melt, which coincided with the melt date of our treatment plots—as a result, we present here data from after that period. During sampling, which continued every 5–14 days until the end of the growing season (for a total of 10 times over the season), a line of 10 yellow, round, open-topped pitfall traps (10 cm diameter) was placed in each plot along a center transect perpendicular to where the fences had been

in the plots over the winter. Traps were left for 24 h, after which time spiders were collected and traps were removed. Importantly, such collections represent an index of abundance, rather than true abundance, since pitfall catches depend on surface activity. On each sampling day, we took point measurements of air and ground temperatures for each plot, calibrating them to a nearby weather station to obtain daily averages.

Collected spiders were pooled by plot and stored in 70 % ethanol for subsequent imaging and identification. A significant proportion of the spiders caught were juveniles and thus they could not be reliably identified to species using standard methods based on genital morphology. As a result, for the purpose of our community analysis, we opted to identify individuals to the level of genus based on other morphological characters and markings using Ubick et al. (2005). For the dominant genus *Pardosa*, we took the additional step of identifying all mature and intact adults ($n = 1{,}265$, 61.1 % of all *Pardosa* specimens) to species using genital morphology (Dondale and Redner 1986)—all identified as a single species, *Pardosa lapponica*. In addition to separating mature male and female *P. lapponica*, we identified juvenile wolf spiders with similar markings to create a putative category of juvenile *P. lapponica* specimens (herein, juvenile) for our analysis. As some of the juveniles in this category may represent other species of wolf spiders, we suggest caution in the interpretation of results for that category. Voucher specimens are available at the Insect & Invertebrate Zoology Museum at the University of Calgary.

Body and ovary mass

Due to the large number of spiders collected ($n = 2{,}811$) and the fragility of spider carcasses when they have been dried, we used a length–mass regression to infer the mass of spiders based on the length of their abdomen following preservation in ethanol. Such length–mass regressions are common in ecological studies involving large numbers of arthropods (e.g., Tulp and Schekkerman 2008) and typically produce accurate estimates of body mass (Sample et al. 1993). Carapace width is often used to infer mass in studies of spiders because it remains constant within a molt and is largely independent of short-term fluctuations in body condition. Because we were interested in testing for differences in mass within a season and within single molts, however, we chose to measure the abdomen, which can fluctuate in size based on food, water, and fecundity (Foelix 1996). The strong relationship between abdomen size and actual body mass in a subset of our specimens (see below) provided further justification for its use to infer body mass in our study.

To measure abdomen length, spiders were removed from ethanol, photographed, and then measured digitally using the program ImageJ (http://rsbweb.nih.gov/ij/). To create a length–mass model relevant to our system, we used 106 spider specimens collected during the 2009 growing season (stored in 70 % ethanol) from a natural population located near our focal sites. Following the measurement of their abdomens, they were oven-dried at 60 C for 5 days and then weighed to the nearest 0.001 mg. We fitted linear ($y = ax + b$), exponential ($y = ae^{bx}$), and power ($y = ax^b$) models to the data, where y equals dry body mass, x is abdomen length, and a and b are the model coefficients. The power model had the best fit ($y = 0.1866$ $x^{2.587132}$; $R^2 = 0.935$, Figure S1), which is consistent with previous findings (Rogers et al. 1976). We fitted the resulting length–mass model to all collected spiders that had not been dissected for identification purposes and that had intact abdomens ($n = 2,344$, 83 % of the specimens collected).

As we did not collect spider eggs during sampling, we could not directly assess the effect of our treatment on spider fitness. Nevertheless, we opted to estimate the effect of increased snow depth on spider reproduction by testing its effects on the mass of ovaries and attached oocytes (herein, ovaries) during egg development. Ovary mass was measured directly, following dissection and drying, from a subsample of *P. lapponica* females ($n = 24$ for each treatment) collected during the peak of the growing season (day of year 186—July 5th), 2 days prior to when females were first observed carrying egg sacs in the surrounding area.

Statistical analysis

Although it was clear from the different melt dates between plot types (see "Results") that our snow fences had increased the amount of snow around treatment plots, we formally tested the effect of fences on snow depth using the nonparametric Wilcoxon rank sum test on the depth measurements we had collected during the winter. We used the same approach to test for differences in daily air and ground temperatures between plot types.

For both the 1-day and 5-day small-scale trench experiments, we used generalized linear models to assess the impact of trench type on total spider catch, specifying Poisson distributions with log link functions.

Our catch data from the main experiment were typical of overdispersed count data and showed a good fit to a negative binomial distribution (minimum chi-squared, $p = 0.82$). We therefore used generalized linear models, specifying a negative binomial distribution with a logit link function, to analyze the relationships between spider catch (abundance), day of year, and treatment for the entire

spider community, each genera separately, and for each stage/sex class of *P. lapponica*. We did not find a significant interaction between these factors in any of our models and thus used additive models to test our hypotheses.

The individual mass data fit a gamma distribution (chi-squared, $p = 0.61$), so we used generalized linear models specifying a gamma distribution with an inverse link function to analyze the impact of day of year and our snow fence treatment. As with our abundance data, we found no significant interaction between the two independent factors and present here the results of our additive models for all spiders together, each genera, and for each stage/sex class of *P. lapponica*, including the putative juvenile specimens referred to previously. Finally, a Wilcoxon rank sum test was used to test for differences in ovary mass between treatments.

The impact of increased winter snow cover on spider community structure was assessed visually using non-metric multidimensional scaling (NMDS; Legendre and Legendre 1998), and statistically using the ANOSIM (Analysis of Similarity; Clarke 1993) procedure to calculate the standardized mean rank difference of between-treatment and within-treatment compositional variation on the pooled seasonal data. Since we were concerned with testing for community-level effects of our treatment throughout the season, we employed the same techniques on the community data from individual sampling days.

To assess the impact of our snow fences on the timing of events in our spider communities, we followed Corbet and Danks' (1973) seasonal milestone approach and used Wilcoxon rank sum tests to compare the dates when plots achieved 25, 50, and 75 % of the seasonal catch between treatments. We also examined phenology in this way across the different stage/sex classes of *P. lapponica*. All analyses were done using R, version 2.15.1 (http://cran.r-project.org/), with the packages "MASS" (Venables and Ripley 2002), "vegan" (Oksanen et al. 2010), and "coin" (Hothorn et al. 2008).

Results

Plots with snow fences had more snow at the end of the winter than those without (Wilcox rank sum test, $n_{control} = n_{treatment} = 6$, $W = 4$, $p = 0.01$) and paralleled the snow depth conditions of nearby shrub sites. Fences increased snow depth differently in each plot ($\bar{x} = 55.75$ cm, $\sigma^2 = 19.92$); however, all treatment plots melted out on June 6, 2010, 14 days (± 12 h) after nearby control plots ($\bar{x} = 25$ cm, $\sigma^2 = 20$), which had also melted out within 12 h of each other. Melt date was therefore taken to be conserved within-treatment types. Air and ground temperatures did not vary between plot types on

any of the sampling days (Wilcox rank sum test, $n_{control} = n_{treatment} = 6$, p always > 0.3).

Our catches from the small-scale trench experiment (Figure S2) largely validated our use of trenches to isolate the larger experimental plots, with spider catches in the "tight" traps significantly lower than those in "open" traps (GLM, $p < 0.01$) for both the 1-day and 5-day trapping periods. "Wide" traps were less effective at excluding spiders than the "tight" traps (GLM, $p = 0.09$ for the 1-day experiment and $p > 0.5$ for the 5-day experiment) but it should be noted that the small-scale trenches were not as deep as our plot trenches, nor did they fill with water (as occurred in our main experiment), and thus they were probably not as effective at preventing migration. Nevertheless, since the smaller trenches did not perfectly exclude spiders from the sampling plots, late-season findings from our study should be treated with caution.

We captured a total of 2,811 adult and juvenile spiders over the season from 10 genera (Table 1). Spiders from the genus *Pardosa* (Family: Lycosidae) were by far the most common, accounting for 73.6 % of all individuals caught, followed by *Xysticus* (Family: Thomisidae) at 7.2 %. Peak spider abundance (Fig. 1) was achieved in both treatment and control plots on July 5 (day of year 186—roughly the midpoint of the growing season), around the same time that tundra bird hatchlings were first observed in the area.

Day of year was a highly significant covariate in our model of total (all genera included) spider community abundance (GLM, $p < 0.001$; see Table S1a for model coefficients), with 95 % confidence intervals that did not cross zero. The snow fences, however, did not have a
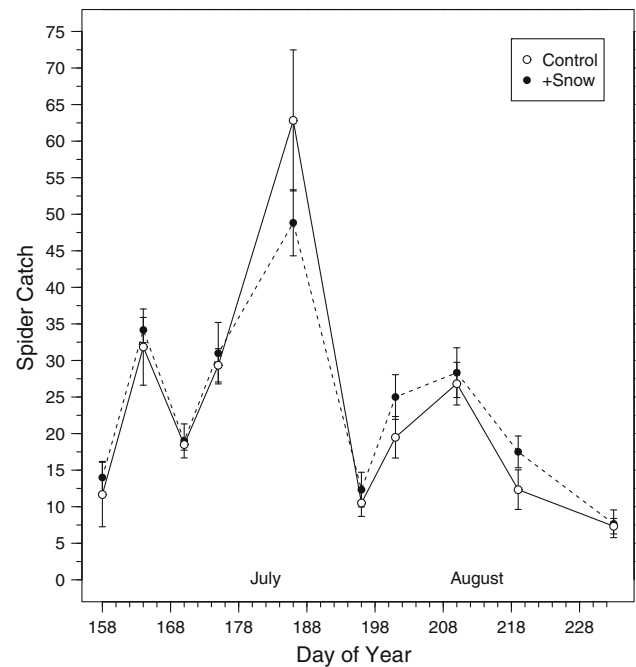

Fig. 1 Spider catch (all genera included) over the season by treatment. *Points* represent the mean catch of spiders during sampling days from control and treatment (+snow) plots, ±standard error

significant effect on abundance for any part of the season (Fig. 1). Consistent with these results, genera-specific models showed a significant effect of day of year but not of treatment type. This pattern also held for the different stage/sex classes of *P. lapponica*, though day of year was not a significant covariate for juveniles.

Table 1 Pooled catches of spider genera and *P. lapponica* stage/sex classes on heath tundra sites over time for control and, in parentheses, treatment plots ($n = 6$ for both)

| Family | Genus | Day of year | | | | | | | | | | Total |
		158	164	170	175	186	196	201	210	219	233	
Clubionidae	*Clubiona*	5 (5)	5 (5)	1 (2)	3 (2)	1 (0)	1 (0)	0 (1)	1 (1)	1 (0)	0 (1)	18 (17)
Gnaphosidae	*Zelotes*	4 (10)	11 (8)	7 (7)	1 (4)	14 (8)	0 (0)	5 (6)	10 (0)	3 (2)	3 (2)	58 (47)
Linyphiidae	*Allomenga*	3 (2)	2 (1)	0 (0)	0 (1)	2 (0)	3 (0)	0 (1)	5 (0)	0 (0)	2 (0)	17 (5)
	Erigone	0 (1)	7 (1)	2 (2)	1 (0)	7 (9)	0 (1)	5 (3)	6 (3)	3 (3)	0 (0)	31 (23)
Lycosidae	*Alopecosa*	1 (1)	11 (10)	2 (5)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (4)	0 (2)	16 (22)
	Arctosa	5 (2)	11 (9)	0 (2)	7 (3)	0 (0)	0 (1)	5 (3)	3 (1)	0 (0)	1 (0)	32 (21)
	Pardosa	31 (53)	89 (103)	87 (80)	143 (154)	326 (234)	56 (67)	81 (116)	110 (134)	52 (83)	35 (35)	1,010 (1,059)
Philodromidae	*Thanatus*	9 (2)	12 (16)	5 (3)	10 (10)	6 (16)	0 (0)	4 (4)	3 (7)	4 (2)	0 (1)	53 (61)
Salticidae	*Sitticus*	1 (0)	21 (34)	1 (7)	0 (0)	0 (10)	0 (1)	4 (4)	10 (14)	6 (4)	0 (1)	43 (75)
Thomisidae	*Xysticus*	11 (8)	22 (18)	6 (6)	10 (12)	21 (16)	3 (4)	13 (12)	13 (10)	4 (7)	3 (4)	106 (97)
Seasonal abundance of the dominant species by stage/sex class												
P. lapponica	Juvenile	16 (22)	14 (22)	6 (3)	13 (13)	35 (26)	31 (23)	13 (28)	37 (33)	12 (17)	6 (11)	183 (198)
	Male	5 (12)	32 (27)	66 (52)	96 (103)	122 (84)	49 (22)	14 (17)	9 (27)	4 (10)	5 (6)	402 (360)
	Female	6 (18)	13 (13)	10 (12)	26 (29)	43 (66)	19 (17)	14 (15)	51 (44)	27 (46)	21 (13)	230 (273)

Genera with fewer than two individuals caught for the entire season and specimens that could not be identified ($n = 52$, 0.02 % of specimens sampled) are not included

Overall, spider community structure, which we defined as the pooled genera-level abundances over the entire season, did not vary by treatment (ANOSIM, $R = -0.1426$, $p = 0.99$; Figure S3a) and, with one exception (day of year 170—June 19), did not vary by treatment on any of the individual sampling days (Figure S3b).

No significant differences between treatments were detected in all three seasonal milestones considered in this study—25, 50, and 75 % of whole-season catches—for any of the spider genera (individually or all together) or any of the *P. lapponica* stage/sex classes (Wilcox rank sum, $n_{control} = n_{treatment} = 6$, p always >0.05). An uneven distribution of *P. lapponica* stage/sex classes among plots meant that we could not formally assess the impact of our snow treatment on sex ratios over time but there were no clear visual differences between treatments in the pooled data (Fig. 2).

Treatment and day of year were statistically significant covariates with the whole-season mass data for the pooled spider genera, with increased snow cover associated with larger individuals. This pattern appeared to be driven by the dominant species *P. lapponica* (GLM, day of year $p = 0.004$ and treatment $p < 0.001$, Table S1e), as neither day of year or treatment were significant when we tested our models separately on each other genus. Of the three stages classes of *P. lapponica* that we examined, day of year was significant only for juveniles (GLM, $p = 0.0006$, Table S1b), while treatment was significant for all stages (Fig. 3, Table S1b-d).
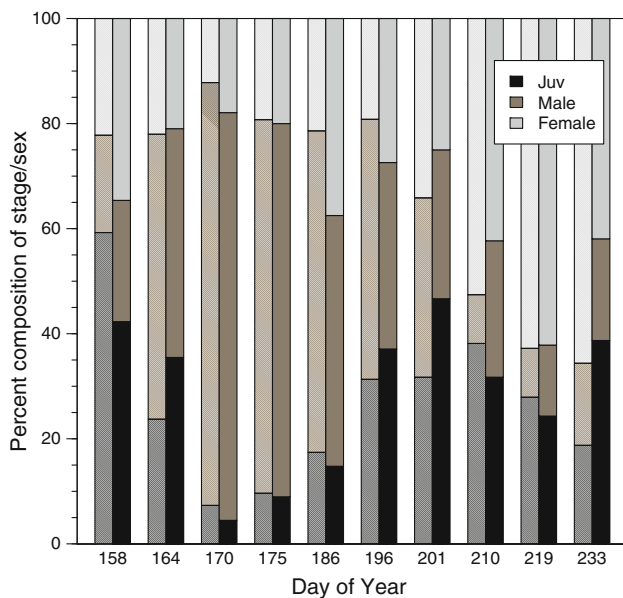

Fig. 2 Proportion of the different stage/sex classes of *P. lapponica* over the season by treatment type. The *lighter set of bars* (*leftside*) represents the pooled stage/sex breakdown of the control plots and the *darker set of bars* is for the treatment plots

Finally, the snow-induced increase in the body mass of female *P. lapponica* appeared to coincide with a significant increase in the ovary mass of the females we examined (Wilcox rank sum, $n_{control} = n_{treatment} = 24$, $W = 190$, $p = 0.02$; Figure S4).

Discussion

Spider abundance in our plots varied over time but was not affected by increased winter snow depth, suggesting that sub-Arctic spiders may be less sensitive to snow cover changes than spiders and other macroarthropods of the high Arctic, which appear to be highly sensitive to melt date (Høye and Forchhammer 2008). We note, however, that absolute emergence time appeared to be affected by our snow treatment due to its effects on melt date as a small number of spiders were observed—but could not be collected using our passive sampling method—on the surface of all plots (control and treatment) within hours of snow melt. Had we been able to capture the small number of spiders active during this period, this may have shifted the dates when different seasonal milestones (25, 50, and 75 % of catch) were achieved in particular plots for some of the rarer genera. The high number of *Pardosa* specimens captured during the remainder of the season, however, suggests that our phenological results for the dominant spider genus in the area are robust in spite of this weakness in our approach.

Spider community structure was also unaffected by the snow fence treatment, consistent with the notion that landscape factors, such as summer vegetation cover, are the primary determinants of spider diversity in northern ecosystems (Bowden and Buddle 2010; Rich et al. 2013). This contrasts with previous work showing that changes in snow cover can quickly alter microarthropod community structure (Dollery et al. 2006) and may be attributable to the short-term nature of our manipulation coupled with the longer generation time of Arctic spiders. It is also possible that our genera-level approach may have been too coarse to detect compositional differences between plots, though we contend that generic richness was likely a close approximation to species richness given the low diversity of Arctic spider assemblages (Marusik and Koponen 2005; Pickavance 2006) and the finding that all mature *Pardosa* individuals identified as a single species. It is also worth noting that snow and temperature manipulation studies in other Arctic and alpine systems have found quantifiable differences in arthropod community structure (Dollery et al. 2006; Hågvar and Klanderud 2009) at coarser taxonomic and temporal scales, suggesting that our season-wide, genera-level approach was not too limiting.

The dominance of *P. lapponica* in our plots is consistent with prior collections around Hudson's Bay (Koponen
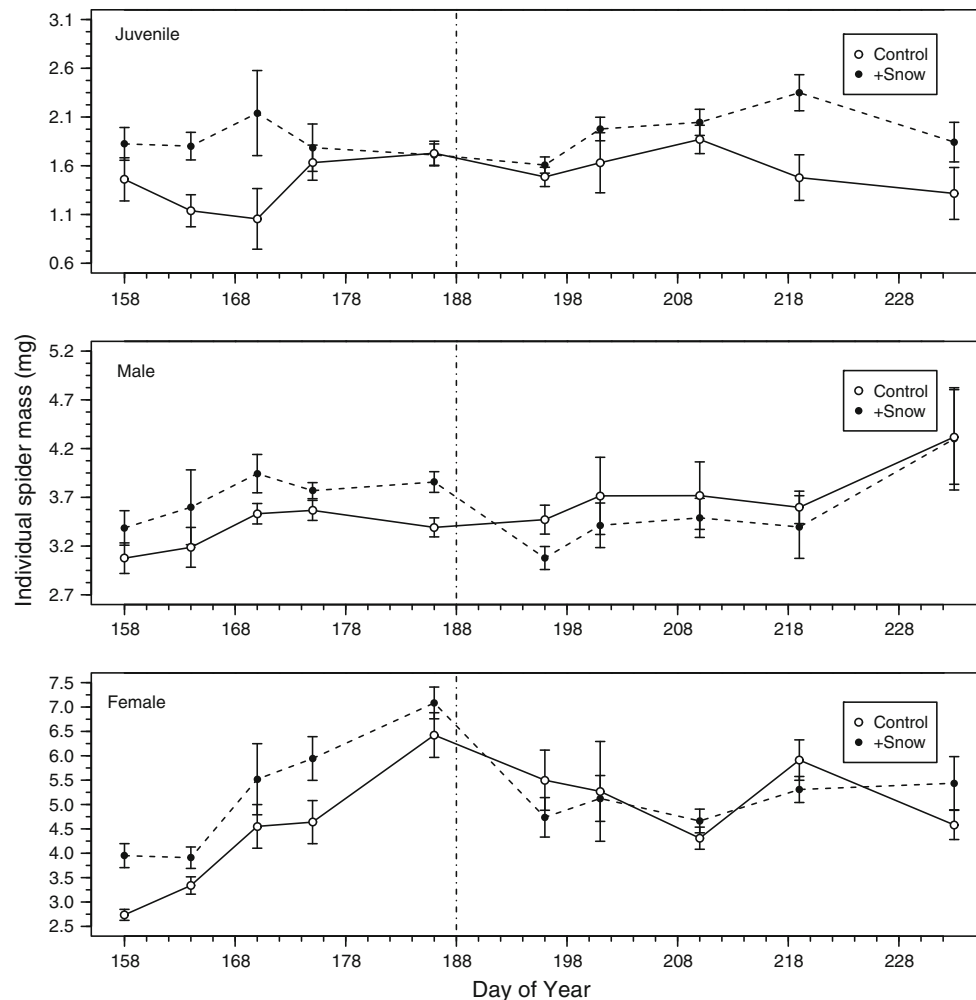
Fig. 3 *P. lapponica* mass over the season by treatment for putative juveniles (*top*), adult males (*middle*), and adult females (*bottom*). *Points* represent the mean individual masses of spiders during sample days from control and treatment (+snow) plots, ±standard error. The *vertical dashed line* represents the day when females carrying egg sacs were first observed in the area

1992; Pickavance 2006) and other low Arctic sites (Bowden and Buddle 2010). In our case, its high relative abundance may have been a product of its active foraging strategy combined with our passive (pitfall) trapping methods. From an ecosystem or food web perspective, such a bias is not problematic as it is likely that foraging birds feed more often on mobile, conspicuous prey.

Since we did not collect spiders or environmental data (other than snow depth) during the winter, we can only speculate on what might have led to the observed mass differences in *P. lapponica* between plot types. A recent 10-year field study of the congeneric spider *Pardosa glacialis* suggests that earlier snow melt is associated with larger adults (Høye et al. 2009), but this may be attributable to temporal autocorrelation in melt dates across sites and the higher growth rates afforded by longer growing seasons in previous years. While our study controlled for previous growing seasons by directly manipulating snow depth, it seems unlikely

that a delay in melt date alone would have resulted in larger spiders given that such a delay necessarily shortens growing season length. Moreover, it seems unlikely that spiders on the control plots would have lost mass during the 14-day interval between melt dates, since prey species (e.g., springtails) were also active during this period, air temperatures were generally low (mean = −0.23 C), and water was abundant across the study area.

We suggest, rather, that the greater mass we observed in *P. lapponica* spiders from the experimental plots arose as a result of thermal changes to the subnivean environment during the winter. Snow is a highly effective insulator and can provide a significant buffer against winter temperature extremes (Sturm et al. 2001b). On heath tundra landscapes such as ours, where winter snow depth is normally quite low (0-0.2 m), 0.5 m of extra snow can reduce daily thermal variability by as much as 80 % (Taras et al. 2002) and increase temperatures at ground level by as much as

10 °C (Sturm et al. 2005). One possibility is that deeper snow created higher subnivean temperatures, allowing spiders to be more active during the winter and to accumulate additional food resources. Prior studies have shown that spiders can actively hunt during the winter and will feed at temperatures as low as −2° C (Norberg 1978; Aitchison 1984; Gunnarsson 1988; Hågvar and Hågvar 2011). It is not known whether the *P. lapponica* in our system are winter-active, but as a genus, they are highly cold-tolerant (Duman et al. 2004; Murphy 2008) and will hunt during the winter in more temperate zones (Edgar and Loenen 1974; Norberg 1978), where average temperatures are comparable with early- and late-season winter temperatures in the sub-Arctic. Under these warmer winter conditions, therefore, *P. lapponica* individuals might have been able to feed on other arthropods known to be active in the subnivean environment, such as mites (*Acari*) and springtails (*Collembola*) (Merriam et al. 1983; Hågvar and Hågvar 2011). Alternatively, or in parallel with the effects of a warmer subnivean environment, a more stable thermal environment may have reduced the high metabolic costs of overwintering (Kotiaho et al. 1999). Relative to stable cold temperatures, repeated cold exposure has been shown to increase the production of costly cryoprotectants in Antarctic midges (Teets et al. 2011), but the effects of such fluctuations on the energy stores and survival of other arthropod species vary considerably and have not been examined for Arctic spiders (review Marshall & Sinclair 2012).

The increase in the proportion of juveniles in the population following day 186 (Fig. 2) coupled with the drop in average adult female body mass (Fig. 3c) and our own observations of spiders carrying egg sacs at the beginning of July suggest to us that this was a significant period of reproduction in the population. We speculate that the early-season gains in female mass provided by our snow treatment were put toward reproduction and may have increased female reproductive success (not directly measured in this study), which is consistent with results from food supplementation experiments (Kreiter and Wise 2001; Wise 2006) and with prior research showing that body size scales with egg size and number in spiders and other arthropods (Berrigan 1991; Marshall 1994). Our observation that *P. lapponica* females in treatment plots had significantly larger ovaries and oocytes than their control counterparts during the peak reproductive period (day of year 188) supports the notion that snow-induced gains to female body mass could lead to higher reproductive success.

This study, which to our knowledge is the first experimental test of the impact of increased winter snow cover on macroarthropod activity at a landscape scale, found that the abundance and diversity of an Arctic spider community was not affected by a single year of snow accumulation.

Interestingly, increased winter snow cover did produce a significant difference in the body mass of *P. lapponica* individuals of all sexes and stages and in the ovary mass of *P. lapponica* females, likely as a result of increased subnivean temperatures during the winter. The precise mechanism behind the mass increase remains to be determined, though it may have arisen as a result of warmer temperatures facilitating winter feeding activities and/or reducing the need to produce costly cold-resistant compounds. The long-term consequences of increased snow cover are also unknown but if the short-term patterns we observed hold, these mass differences could lead to differential reproductive success between shrubby and shrub-free sites, affecting spider abundance and the availability of prey to migrant birds in the Arctic.

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