

Impacts of female body size on cannibalism and juvenile abundance in a dominant arctic spider

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Funding information

Conservation, Research and Education Opportunities International; Lewis and Clark Fund; Arctic Institute of North America; National Science Foundation, Grant/Award Number: 1210704; Alaska Geographic; Discover Denali Research Fellowship; National Geographic Society; Kappa Delta Foundation

Handling Editor: Eoin O'Gorman

Abstract

1. Body size influences an individual's physiology and the nature of its intra- and interspecific interactions. Changes in this key functional trait can therefore have important implications for populations as well. For example, among invertebrates, there is typically a positive correlation between female body size and reproductive output. Increasing body size can consequently trigger changes in population density, population structure (e.g. adult to juvenile ratio) and the strength of intraspecific competition.
2. Body size changes have been documented in several species in the Arctic, a region that is warming rapidly. In particular, wolf spiders, one of the most abundant arctic invertebrate predators, are becoming larger and therefore more fecund. Whether these changes are affecting their populations and role within food webs is currently unclear.
3. We investigated the population structure and feeding ecology of the dominant wolf spider species *Pardosa lapponica* at two tundra sites where adult spiders naturally differ in mean body size. Additionally, we performed a mesocosm experiment to investigate how variation in wolf spider density, which is likely to change as a function of body size, influences feeding ecology and its sensitivity to warming.
4. We found that juvenile abundance is negatively associated with female size and that wolf spiders occupied higher trophic positions where adult females were larger. Because female body size is positively related to fecundity in *P. lapponica*, the unexpected finding of fewer juveniles with larger females suggests an increase in density-dependent cannibalism as a result of increased intraspecific competition for resources. Higher rates of density-dependent cannibalism are further supported by the results from our mesocosm experiment, in which individuals occupied higher trophic positions in plots with higher wolf spider densities. We observed no changes in wolf spider feeding ecology in association with short-term experimental warming.
5. Our results suggest that body size variation in wolf spiders is associated with variation in intraspecific competition, feeding ecology and population structure. Given the widespread distribution of wolf spiders in arctic ecosystems, body size shifts in these predators as a result of climate change could have implications for lower trophic levels and for ecosystem functioning.

KEYWORDS

Arctic, body size, cannibalism, density dependence, feeding ecology, population structure, stable isotope, wolf spider

1 | INTRODUCTION

Changes in animal body size have been extensively documented across taxa in association with recent and historic climate change (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011). While many ectothermic taxa become smaller with increasing temperature (Daufresne, Lengfellner, & Sommer, 2009), some become larger (Bowden, Hansen, Olsen, & Høye, 2015; Chamaillé-Jammes, Massot, Aragón, & Clobert, 2006; Høye, Hammel, Fuchs, & Toft, 2009). Shifts in body size should have particularly strong effects on ectothermic invertebrates because nearly all physiological processes in this group scale with size, including metabolism, consumption, growth and fecundity (Chown & Gaston, 2010; Honěk, 1993; Kalinkat, Jochum, Brose, & Dell, 2015). Moreover, because size dictates the nature of many intra- and interspecific interactions (Brose et al., 2006; Kalinkat et al., 2013), body size changes are likely to affect not only the population structure and stability of these individual species (De Roos, Persson, & McCauley, 2003; Persson & de Roos, 2013) but also ecosystem properties like community structure and food web dynamics (Brose et al., 2012; Woodward et al., 2005).

Juvenile recruitment and population density are two key determinants of the long-term health of a population that can be influenced by body size. Among arthropods, female fecundity is typically positively correlated with body size (Fox & Czesak, 2000; Honěk, 1993), suggesting that larger females could lead to higher population densities. Alternatively, larger body sizes could increase the intensity of competition for resources, leading instead to lower equilibrium population densities (e.g. Belgrano, Allen, Enquist, & Gillooly, 2002; Savage, Gillooly, Brown, West, & Charnov, 2004). Regardless, the expected increase in reproductive output by larger females also has the potential to shift the age and size structure of a population to one with a greater proportion of small, young individuals relative to larger, older ones. Such shifts in population structure can affect local population dynamics due to altered competitive interactions between different age cohorts (Nisbet & Onyiah, 1994). For example, in species that use the same resource pool across life stages, higher reproductive rates can result in fewer per-capita resources, thereby promoting behaviours associated with exploitative competition, such as cannibalism (Fox, 1975). This scenario is especially likely for species that have overlapping generations, because cannibalism is more likely to occur when there is increased size disparity between individuals (Polis, 1988).

The rate of warming in the Arctic far exceeds the global average (Overland et al., 2017), making tundra ecosystems among the fastest changing regions on Earth. This warming has already been linked to body size changes in several species of arctic arthropods (e.g. Bowden,

Eskildsen, et al., 2015; Bowden, Hansen, et al., 2015; Høye et al., 2009), a group which is expected to be highly vulnerable to environmental change (Devictor et al., 2012; Thackeray et al., 2016; Warren, Price, Graham, Forstenhaeusler, & VanDerWal, 2018). For example, wolf spiders, one of the most widespread and locally abundant predators across the Arctic (Høye & Forchhammer, 2008b; Koltz, Asmus, Gough, Pressler, & Moore, 2018; Wyant, Draney, & Moore, 2011), are becoming larger and hence, more fecund in response to earlier spring snowmelt (Høye et al., 2009; J. J. Bowden, unpubl. data). Under these conditions, cannibalism could become an important regulating mechanism of population density because these animals are known to be density-dependent cannibals (e.g. Buddle, Walker, & Rypstra, 2003; Wagner & Wise, 1996; Wise, 2006). In the Arctic, wolf spiders exhibit overlapping generations year-round due to their extended life history (Dondale & Redner, 1990), making them a particularly promising system for exploring such population-level consequences of body size variation. A better understanding of how body size variation influences wolf spider population dynamics is also relevant at regional and global scales, because the Arctic contains much of the global pool of soil organic carbon (Tarnocai et al., 2009), and changes in the density of these key tundra predators can indirectly alter decomposition rates and soil nutrients (Koltz, Classen, & Wright, 2018).

We leveraged natural variation in body size between two nearby populations of a dominant wolf spider species, *Pardosa lapponica* (Thorell 1872), in the Alaskan Arctic to investigate how female body size relates to population structure and feeding ecology. Specifically, we asked whether juvenile abundance, female abundance and feeding ecology differ between the two sites. Body size in *P. lapponica* is positively correlated with fecundity (Bowden & Buddle, 2012a), so we expected that juvenile abundance would be positively associated with larger adult females. Previous work from these areas indicate that total wolf spider abundances may be higher at the site with larger females (Gough, 2012; Rich, Gough, & Boelman, 2013; A. Asmus, unpubl. data), suggesting that competition and density-dependent cannibalism could be higher there as well. Thus we predicted that spiders from the site with larger females would be at a higher trophic position due to their ability to consume larger prey (including other predators) and their increased opportunity for cannibalism on juvenile wolf spiders. In addition to the field population comparison, we experimentally tested the assumption that higher wolf spider densities lead to higher rates of density-dependent cannibalism (Buddle et al., 2003; Wise, 2006) and asked whether warmer temperatures alter this behaviour. Specifically, we isolated the effects of density and warming on wolf spider feeding ecology by manipulating wolf spider density under ambient and artificially warm temperatures in field-based mesocosms. Similar to our predictions for the field

populations, we expected that individuals from plots with higher wolf spider densities would exhibit higher trophic positions than those from low wolf spider density plots but that the source of basal resources would not differ between treatments. We also expected that wolf spiders exposed to experimental warming would be at higher trophic positions than spiders from ambient temperature plots due to higher activity levels (Kruse, Toft, & Sunderland, 2008) and that consequently, there would be more potential opportunities for antagonistic interactions and intraguild predation to occur under warming (e.g. Koltz, Classen, et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Field sampling

We sampled wolf spider communities at two arctic tundra sites, Toolik (68°65'N, 149°58'W) and Imnavait (68°62'N, 149°30'W) in 2012. The sites are 10.4 km apart in the northern foothills of the Brooks Range, Alaska, near Toolik Lake Field Station. The open tundra areas at Toolik and Imnavait are characterized by similar plant communities and abiotic conditions, with the exception that Imnavait has slightly warmer average summer temperatures than Toolik and experiences spring snowmelt a few days later (Rich et al., 2013; Sweet, Gough, Griffin, & Boelman, 2014). We accounted for these seasonal differences between the sites and their potential effects on spider phenology by standardizing the timing of our sampling according to snowmelt date. At each site, we sampled wolf spiders 2 weeks, 1 month and 2 months after snowmelt had occurred. Table S1 contains the dates of sampling, spring snowmelt and fall snow accumulation during the study year.

Two weeks and 1 month past snowmelt, we sampled each site using pitfall traps placed 1 m apart on a grid of 10 m × 10 m. Due to concerns about depleting the local population and potential low sample sizes during the latter part of the season, at 2 months past snowmelt, we sampled adjacent areas at each site using four 5 m × 5 m grids of pitfall traps; each grid was separated by at least 30 m. Thus at each sampling time point, there were 100 pitfall traps per site. Weather affects wolf spider activity and catch densities (Høye & Forchhammer, 2008a), so we tried to sample only on sunny days. Pitfall traps contained 75% ethanol and were left out for 24 hr during each sampling period, except during the sampling at one month past snowmelt at Imnavait, where traps were open for 48 hr due to unforeseen poor weather. We therefore only used pitfall catch data from 15 and 60 days past snowmelt to compare abundances of females between sites (see below).

2.2 | Sample processing

We identified all adult female specimens from Toolik and Imnavait to species according to Dondale and Redner (1990), except for the classification of *Pardosa concinna* and *Pardosa lapponica*, which are likely to

be the same species (Sim, Buddle, & Wheeler, 2014). Juveniles cannot be identified to the species level by morphology alone. As in Sackett, Buddle, and Vincent (2008), we assume that the relative abundance of juveniles of each species reflects that of the adult community. To compare body sizes (and hence, reproductive potential) at each site and to relate body size to trophic position, we measured the carapace width (Hagstrum, 1971; Pickavance, 2001) of every adult female and juvenile wolf spider using digital callipers (Diesella). Parasitism of wolf spider egg sacs by parasitoid wasps also affects reproductive output by female spiders, and this can occur more often within the larger egg sacs produced by larger females (Bowden & Buddle, 2012b). Thus, we dissected all egg sacs present from females sampled at Toolik and Imnavait in order to estimate parasitism rates at the two sites.

2.3 | Mesocosm experiment

We conducted a fully factorial mesocosm experiment during June–July 2013 near Toolik Field Station to measure the effects of altered wolf spider densities and warming on wolf spider feeding ecology (Figure S1). The mesocosms were 1.5 m in diameter and enclosed with aluminium flashing that was buried 20 cm belowground and stood 20 cm above the soil surface. Plots were distributed among five blocks and randomly assigned to one of six spider density/warming treatments for a total of 30 plots (see Koltz, Classen, et al., 2018).

For the warming treatment, we covered the mesocosm openings with heavy gauge plastic sheeting that had regularly spaced, small openings to allow the passage of air and rainfall. We measured temperature at the soil surface in the plots every half hour from 12 June to 22 July using iButtons (Maxim Integrated). Temperatures during this period were significantly higher in the experimentally warmed plots than in the ambient temperature plots (mixed effects model with plot nested in block; warming treatment: Estimate ± SE = 2.223 ± 0.381, $df = 27$, $t = 5.845$, $p < 0.0001$). Mean temperatures in the ambient temperature plots were 15.23 (±2.35 SE)°C and those in the warmed plots were 17.45 (±2.95 SE)°C (Figure S2).

The spider density treatments included: (a) reduced wolf spider density, (b) control wolf spider density and (c) high wolf spider density. We removed all wolf spiders from the reduced density plots at the beginning of the summer and continued to check and remove individuals throughout the experiment. High-density plots received enough additional spiders at the start of the experiment to bring wolf spider densities to approximately double the early season average density of control plots. We used pitfall traps at the end of July to verify that we had successfully manipulated wolf spider densities (ANOVA: $F_{2,27} = 6.20$, $p = 0.0061$). Post-hoc Tukey tests for these data showed that high density plots had significantly more spiders than either low density ($p = 0.0061$) or control plots ($p = 0.044$), although densities did not differ between low and control density plots ($p = 0.68$; Figure S3a). Density estimates from the pitfall traps showed that there was an average of 0.3 ± 0.48 wolf spiders in low density plots, 0.6 ± 0.7 wolf spiders in control plots, and 1.5 ± 1.08 wolf spiders in the high density plots. At the conclusion of the

experiment, we destructively sampled the plots in order to opportunistically catch any remaining wolf spiders. We measured the body sizes (carapace width) of these specimens and of the wolf spiders caught earlier in pitfall traps and removed the legs from a subset of individuals for stable isotope analyses.

2.4 | Wolf spider feeding ecology

We used stable isotope analyses of carbon (C) and nitrogen (N) to quantify the functional feeding roles of a subset of juveniles and non-egg sac carrying adult female *P. lapponica* from the Toolik and Imnavait field populations. We also conducted stable isotope analyses on all captured wolf spiders from the mesocosm experiment. The ratio of $^{13}\text{C}/^{12}\text{C}$ is generally accepted to be indicative of the source of basal resources within the food web, while the ratio of $^{15}\text{N}/^{14}\text{N}$ is indicative of trophic position (Post, 2002). Because it provides information on trophic level, $\delta^{15}\text{N}$ is a useful measure of relative intraguild predation or cannibalism (Rickers, Langel, & Scheu, 2006; Wise, Moldenhauer, & Halaj, 2006), whereby higher values of $\delta^{15}\text{N}$ among individuals of the same species suggest higher consumption rates of other predators. While sample storage in ethanol can affect carbon stable isotope ratios in invertebrates (Sticht, Schrader, & Gieseemann, 2006), we assume here that any effects of ethanol storage were similar across samples and experimental treatments. We also measured the stable isotope ratios of a subset of Collembola that were removed from pitfall traps to use as site-specific isotopic baselines for Toolik and Imnavait (see Ponsard & Ardit, 2000). We used Collembola as our isotopic baseline because this group is an important prey source for wolf spiders (Koltz, Classen, et al., 2018; Wise, 2004), and because as detritivores, they should reflect differences in $\delta^{13}\text{C}$ between the two sites due to any differences in vegetation. We express values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for the field-collected wolf spiders from Toolik and Imnavait as the measured values minus the site-specific mean value for Collembola.

Wolf spider and Collembola specimens were dried for 48 hr at 60°C and homogenized with a mortar and pestle prior to stable isotope analysis. We used whole bodies of specimens from the Toolik and Imnavait field populations and between 4–6 legs from wolf spiders collected from the mesocosm experiment. Because of their small size, up to 13 Collembola were pooled per sample. Stable isotope ratios of animals were then determined at the Duke Environmental Stable Isotope Laboratory (DEVIL) using a Carlo-Erba NA1500 elemental analyser feeding a Thermo Finnigan Delta Plus XL continuous flow mass spectrometer system. Ratios were calculated as δX in per ml (vs. atmospheric N_2 for ^{15}N and vs. VPDB for ^{13}C) as $((R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}) \times 1,000$, whereby R represents the heavy to light isotope ratio (i.e. $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) and X is the target isotope. Reference materials from The National Institute of Standards and Technology (NIST) and the U.S Geological Survey (USGS), as well as internally calibrated standards were used for 3-point normalization of raw isotope data. The ratio of standards to samples analysed was approximately 1:6.

2.5 | Analyses

We conducted all statistical analyses in R (R Core Team, 2017). We assessed differences in adult female body size between the field populations at Toolik and Imnavait by fitting a linear model with site and sampling date (days since snowmelt) as the predictors.

We used a hurdle model (Cameron & Trivedi, 2005, 2013; Mullahy, 1986) to model the counts of observed juveniles at Toolik and Imnavait as a function of the number of adult females captured in a trap (of the dominant species *P. lapponica*; Table S2), the average size of those females, sampling date, site and sampling grid size (small/large) using the R package *pSCL* (Zeileis, Kleiber, & Jackman, 2008). Hurdle models are ideal for analysing count datasets that exhibit more or less zero values than expected by a traditional Poisson process because they model the probability that we will observe any non-zero count (in this case, juveniles in a trap) independently from the potential value of that count (i.e. the actual number of juveniles we are likely to see). We also used a separate hurdle model to test for differences in the abundance of adult females as a function of site and sampling grid size. We used trap-level counts of the dominant female species (*P. lapponica*) that were sampled 15 and 60 days past snowmelt (the two periods for which traps were deployed for 24 hr). For both of the hurdle models, we used a binary logit model for the zero-hurdle model and a truncated Poisson model for the count model. In each case, we began with fully parameterized models for both the zero-hurdle model and the count model and proceeded to eliminate non-significant terms one at a time until achieving the simplest possible model.

We tested for site-specific differences in stable isotope ratios by fitting separate linear models for values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from wolf spiders collected from Toolik and Imnavait. The main effects in the models included site, body size and the number of days since snowmelt. Adult females that were analysed for stable isotopes included reproductively mature *P. lapponica* that were sampled at 15, 30 and 60 days past snowmelt at each site; all analysed juveniles were collected 30 days after snowmelt. Due to the uncertainty in species composition of juvenile wolf spiders, we conducted these analyses separately for adult females and juveniles.

To test the influence of our experimental treatments on wolf spider body $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, we estimated linear mixed effects models through the *lmer* function of the *LME4* and *LMERTEST* packages (Bates, Maechler, Bolker, & Walker, 2014; Kuznetsova, Brockhoff, & Christensen, 2017). The wolf spider density treatment, the warming treatment and individual body size (carapace width) were included as main effects in these models; treatment block was included as a random effect. Although life stage may also be related to feeding ecology, it was not included as an additional predictor variable in these models, because body size and life stage are highly correlated (i.e. adults are larger than juveniles) and because AIC values were substantially better for all models that included body size as compared to those that included life stage. In order to account for variation in the actual wolf spider densities in each of the pre-assigned treatments, we also repeated this analysis by replacing the wolf spider treatment categories (i.e. low, control, high) with the

explicit measures of wolf spider density that were collected using pitfall traps at the conclusion of the experiment (i.e. spider density was a continuous predictor in this alternate model). We simplified all models by sequentially eliminating non-significant interaction terms one at a time, followed by non-significant main effects.

3 | RESULTS

3.1 | Field populations

We collected and measured a total of 575 wolf spiders from the two sites (Toolik $N = 338$; Imnavait $N = 237$). Based on identifications of mature females, we determined that wolf spider communities from both sites are >95% comprised of a single species, *Pardosa lapponica* (Table S2).

Adult female *P. lapponica* were significantly larger at Imnavait than at Toolik (Figure 1a; average female body size: Imnavait = 2.217 ± 0.137 cm, Toolik = 2.164 ± 0.142 cm; LM, Toolik site (reference category: Imnavait): -0.0655 ± 0.03024 , $t = -2.166$, $p = 0.032$). The results of our hurdle model for juveniles indicate that while none of the variables explored predict the number of juveniles in our traps, the possibility of observing any juveniles at all increased in later sampling dates (Estimate \pm SE = -0.047 ± 0.013 , $z = 3.763$, $p < 0.001$) and decreased as a function the average size of females

(Estimate \pm SE = -0.765 ± 0.191 , $z = -4.018$, $p < 0.001$; Figure 1b; Table 1). The results of the hurdle model for abundances of adult female *P. lapponica* indicate that traps are more likely to capture females at Toolik than at Imnavait. We interpret this result as indicative of a higher abundance of females at Toolik (Figure 1c; Table S3). We found no evidence of egg sac parasitism rates being different between the sites (proportion of egg sacs parasitized: Imnavait = 16%, Toolik = 14%; LM with binomial errors, Intercept: -1.67 ± 0.44 , $z = -3.76$, $p = 0.0001$; Toolik site (reference category: Imnavait): -0.15 ± 0.63 , $z = -0.23$, $p = 0.817$; Figure 1d).

In terms of differences in feeding ecology between the sites, we found that adult female *P. lapponica* and juvenile wolf spiders from Imnavait were significantly more enriched in both ^{15}N and ^{13}C than those from Toolik (Figure 2a; Table 2; Table S5 for raw isotope values by site and life stage). Body size was not a significant predictor of either trophic position ($\delta^{15}\text{N}$) or basal resources ($\delta^{13}\text{C}$) in the adult female or juvenile spiders (Table 2). Stable isotope values were also not predicted by date of snowmelt in the adult females (Table 2).

3.2 | Density and warming experiment

At the end of the experiment, wolf spiders collected from high-density and control-density plots were significantly larger than spiders from low-density plots (Table S4; Figure S3b). The results of our mixed effects models show that larger wolf spiders were more

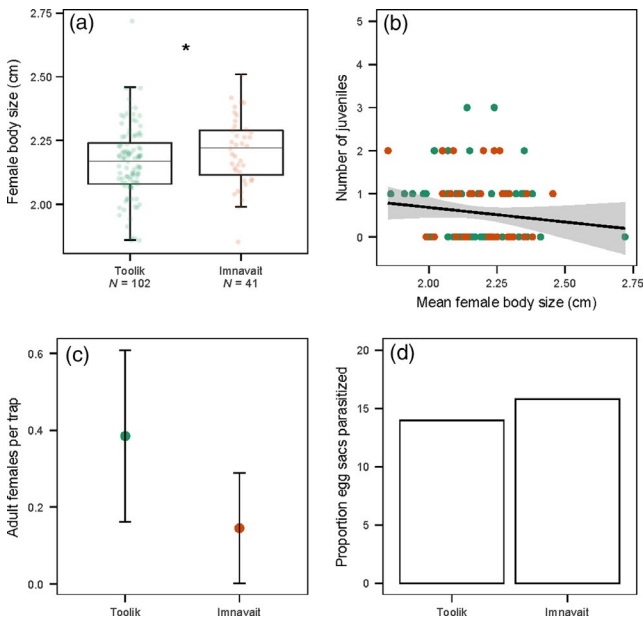


FIGURE 1 (a) Female body size is smaller at Toolik than at Imnavait in the dominant species of wolf spider *Pardosa lapponica*. (b) There is a negative association between trap-level counts of juvenile wolf spiders and mean female body size of *P. lapponica* at Toolik (green) and Imnavait (orange). Panel (c) shows the abundance of females per trap from the two sites. (d) Rates of egg sac parasitism among wolf spiders are similar at Toolik (14%) and Imnavait (16%). Body size is expressed as carapace width in cm. The abundances in (c) are pitfall-level catches of wolf spiders that were sampled 15 and 60 days past snowmelt at each site

TABLE 1 Results of hurdle model for counts of observed juvenile wolf spiders as a function of the number of females captured in a trap, the average size of those females, sampling date past snowmelt, site (Toolik or Imnavait), and the size of the sampling grid. Adult females were reproductively mature female *Pardosa lapponica*, which is the dominant species of wolf spider at both study sites (Table S2). Both models were simplified by eliminating non-significant predictors one by one

Predictor	Estimate	SE	z	p-Value
Count model (truncated Poisson with log link)				
Intercept	-0.560	0.248	-2.261	0.024
Number females	—	—	—	ns
Mean female size	—	—	—	ns
Sampling date	—	—	—	ns
Sampling grid type (small)	—	—	—	ns
Site (Toolik)	—	—	—	ns
Zero hurdle model (binomial with logit link)				
Intercept	—	—	—	ns
Number females	—	—	—	ns
Mean female size	-0.765	0.190	-4.018	<0.0001
Sampling date	0.047	0.013	3.763	0.0002
Sampling grid type (small)	—	—	—	ns
Site (Toolik)	—	—	—	ns

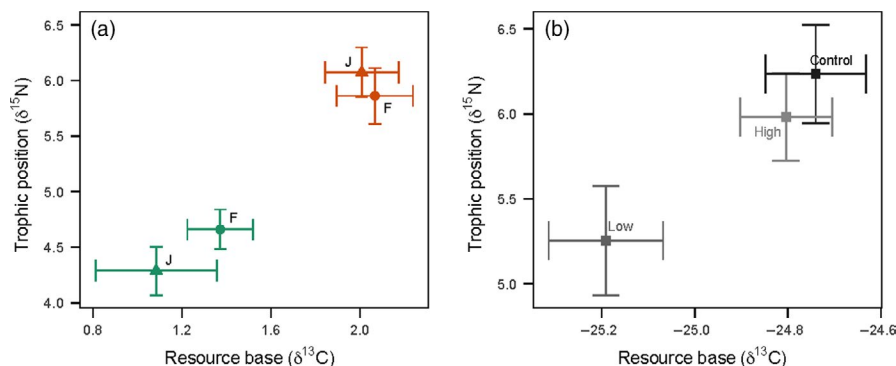


FIGURE 2 (a) Mean \pm SE of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for adult female and juvenile *Pardosa lapponica* from the Toolik (green) and Imnavait (orange) study sites. 'F' and 'J' denote the isotopic values for female and juvenile wolf spiders, respectively. (b) Mean \pm SE of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for wolf spiders collected from experimental mesocosm plots with low, control, or high densities of wolf spiders. Axes scales differ between panels because individual wolf spiders from field populations in (a) were standardized by site-specific mean Collembola isotopic values (Table S5), while those from the experimental plots in (b) are presented as the raw values

TABLE 2 Results of linear models for variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in juvenile and adult female wolf spiders *Pardosa lapponica* from the two study sites. Females were collected 15, 30, or 60 days past snowmelt (SM) at each site, while juveniles were collected 30 days past snowmelt. Body size of all individuals was measured as carapace width, and raw values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were corrected by the mean isotopic values of Collembola from the same sites (Table S5). The reference site in all models is Imnavait; models were simplified by eliminating non-significant predictors one by one

Response	Predictor	Estimate	SE	t	p-Value
Female $\delta^{15}\text{N}$	Intercept	5.86	0.19	31	<0.0001
	Body size	—	—	—	ns
	Time since SM	—	—	—	ns
	Site (Toolik)	-1.20	0.26	-4.67	<0.0001
Female $\delta^{13}\text{C}$	Intercept	2.07	0.24	8.59	<0.0001
	Body size	—	—	—	ns
	Time since SM	—	—	—	ns
	Site (Toolik)	-0.70	0.27	-2.57	0.020
Juvenile $\delta^{15}\text{N}$	Intercept	6.07	0.15	40.73	<0.0001
	Body size	—	—	—	ns
	Site (Toolik)	-1.78	0.21	-8.47	<0.0001
Juvenile $\delta^{13}\text{C}$	Intercept	2.01	0.15	13.22	<0.0001
	Body size	—	—	—	ns
	Site (Toolik)	-0.92	0.21	-4.30	<0.0001

TABLE 3 Mixed-effects model results for variation in values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in wolf spiders collected from experimental mesocosm plots that either had low, control or high densities of wolf spiders. The reference category for wolf spider density (SD) is low density; Table S6 shows model results with the reference category as control wolf spider density and Table S7 shows model results using the realized densities of wolf spiders in place of the pre-assigned treatments. Experimental block was included as a random effect. The models were simplified by eliminating non-significant predictors one by one

Response	Predictor	Estimate	SE	df	t	p-Value
$\delta^{15}\text{N}$	Intercept	3.232	0.475	42	6.80	<0.0001
	Body size	0.453	0.091	42	4.99	<0.0001
	Control SD	0.584	0.288	42	2.03	0.0488
	High SD	0.496	0.255	42	1.94	0.0585
	Warming	—	—	—	—	ns
	Experimental block	—	—	—	—	ns
$\delta^{13}\text{C}$	Intercept	-25.617	0.220	42	-116.26	<0.0001
	Body size	0.097	0.045	42	2.17	0.0360
	Control SD	0.413	0.134	42	3.09	0.0035
	High SD	0.325	0.122	42	2.66	0.0111
	Warming	—	—	—	—	ns
	Experimental block	—	—	—	—	ns

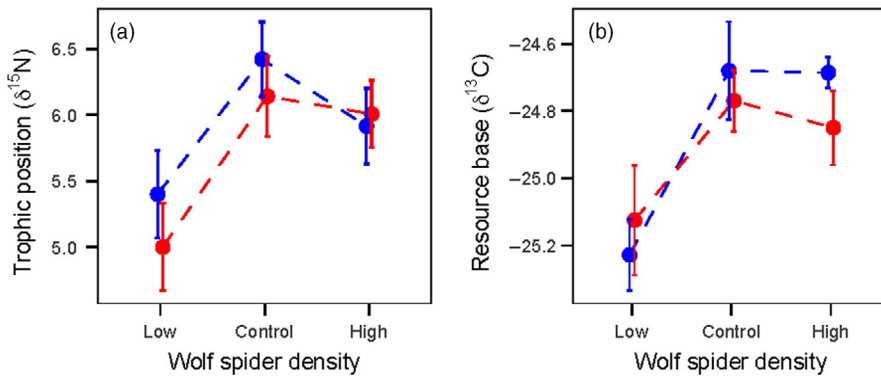


FIGURE 3 Experimentally increasing wolf spider density resulted in a shift of $\delta^{15}\text{N}$ (trophic position) and $\delta^{13}\text{C}$ (resource base). The isotopic niche of wolf spiders from experimentally warmed plots (red) did not differ from those in ambient plots (blue) after one summer of warming

enriched in both ^{13}C and ^{15}N (Table 3; Table S6). After accounting for these body size effects, we found that wolf spiders collected from low-density treatment plots were significantly less enriched in ^{15}N than spiders from plots with control densities and marginally less enriched than those from high-density plots (Figure 2b; Table 3; Tables S5 and S6). Wolf spiders from low-density plots were also significantly less enriched in ^{13}C than those from control and high-density plots. Experimental warming was not significantly related to spider body content of ^{13}C or ^{15}N (Figure 3). Furthermore, our analyses of these data using actual wolf spider densities rather than the categorical characterization of our experimental treatments show that trophic position is indeed positively associated with wolf spider density. Specifically, wolf spiders collected from plots with higher realized spider densities were significantly more enriched in ^{15}N after accounting for body size (Figure S4; Table S7). When realized wolf spider densities were taken into account, we found no effect of density on ^{13}C enrichment in the wolf spiders (Table S7).

4 | DISCUSSION

The insights from this study call into question the basic assumption that larger females with higher fecundity will contribute positively to population growth rates in invertebrates. Body size is well known to be phenotypically plastic in wolf spiders and to be responsive to environmental conditions (e.g. Ameline et al., 2018; Høye & Hammel, 2010; Høye et al., 2009; Legault & Weis, 2013) and prey availability (Reed & Nicholas, 2008). Our study suggests that the indirect consequences of such body size changes include variation in wolf spider population structure and feeding ecology. Such responses, likely due to increased intraspecific competition (Balfour, Buddle, Rypstra, Walker, & Marshall, 2003; Wagner & Wise, 1996), could outweigh the well-known fecundity benefits of larger females and result in unexpected population structures.

Larger female body sizes are typically expected to lead to greater reproduction in invertebrates (Marshall & Gittleman, 1994; Simpson, 1993) and thereby to potential improvements in population viability. Yet, while reproductive output is positively correlated with female body size in *P. lapponica* (Bowden & Buddle, 2012a), we found that the presence of larger females in this species is actually associated with fewer juvenile wolf spiders. The negative correlation between

female size and juvenile presence cannot be explained in this case by a possible preference for larger wolf spider egg sacs by parasitic wasps (Bowden & Buddle, 2012a), because egg sac parasitism rates were not found to differ between our sites (Figure 1d). Alternatively, the negative effect of female size on juvenile survival may be a product of increased cannibalism, because as females become larger and produce more offspring, intraspecific competition for resources increases.

The potential role of cannibalism as a mechanistic explanation for our findings is supported by our experimental result that wolf spiders exhibit higher trophic positions at higher densities (Figures 2b and 3; Table 3; Tables S6 and S7). Cannibalism and intraguild predation are common outcomes of interference competition among natural populations as a result of increased competition for resources (Fox, 1975). Cannibalism provides more resources to larger individuals but also has the indirect effect of reducing the intensity of exploitative competition among conspecifics (Polis, 1988). Cannibalism occurs more frequently when there is greater asymmetry in size between individuals (e.g. Polis, 1988) and has repeatedly been shown to be common across wolf spider species (Buddle et al., 2003; Rypstra & Samu, 2005; Samu, Toft, & Kiss, 1999; Wise, 2006). We note that while body size was positively related to trophic position in the experimental spiders (Table 3), as has been previously observed in spiders (Sanders, Vogel, & Knop, 2015), it was not a significant predictor of isotopic values in the field populations (Table 2). One explanation for this is that because high-density treatments were designed to double the densities of control plots, extreme intraspecific competition in those plots may have resulted in even higher rates of cannibalism among larger individuals. In the field populations, however, our results suggest that body size effects on feeding ecology may be more indirect (i.e. via changes in fecundity and consequently, on density and intraspecific competition). This is supported by the finding that in the field populations, adults and juveniles utilized the same resource space (i.e. had comparable values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; Figure 2a). The similarity in isotopic values between adults and juveniles suggests that spiders in different life stages compete directly for resources and that at least in field settings, smaller juvenile spiders may be as likely to partake in cannibalism and intraguild predation as larger spiders. Wolf spiders from northern latitudes have extended life histories (Buddle, 2000), and their populations can therefore include two to three different size classes within a single habitat at any given time

during the growing season (Dondale, 1961). The large variation in age and size structure of these arctic populations thus provides many opportunities for cannibalism, both for adults on juveniles and for larger juveniles on smaller and younger individuals.

Because our experiment lasted a single summer and arctic wolf spiders have a mean life span of 2 years (Dondale & Redner, 1990), the manipulations likely do not inform us about the effects of density or warming on body size but rather about the potential short-term effect of these treatments on feeding ecology. Nevertheless, we note that wolf spiders collected from high- and control-density plots were larger than those from low-density plots (Table S4; Figure S3b). Density treatments were maintained throughout the summer, so it is not possible to distinguish whether higher density plots had larger spiders as a result of the treatments or due to the density manipulation itself. For example, previous work on density-dependent cannibalism in wolf spiders has shown that survival rates are low under high-density conditions and that wolf spiders that do survive high-density conditions tend to be larger on average than those in lower density conditions (Buddle et al., 2003). It is also possible that the trend toward larger spiders in control and high-density plots could have been an unintended consequence of the manipulation. Specifically, because larger bodied spiders are more conspicuous, the regular removal of wolf spiders from low-density plots could have been inadvertently biased toward larger spiders, thereby resulting in low-density plots having a higher proportion of small spiders. Although the shift in feeding ecology that we observe with increasing spider density could be partially due to the trend in more large bodied spiders in control and high density plots, we are reasonably confident that our experimental findings reflect an effect of density on diet, because body size variation was accounted for in all models that tested for treatment effects on isotopic composition (i.e. on levels of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$; Table 3).

The full shift in feeding ecology that occurred under higher wolf spider densities suggests that cannibalism is not a preferred dietary choice but rather a direct result of increased intraspecific competition. Specifically, we found that wolf spiders experience a shift in trophic position ($\delta^{15}\text{N}$) and resource base ($\delta^{13}\text{C}$) both under higher density experimental conditions (Figure 2b) and in field conditions where adults are larger and reproductive rates are higher (Figure 2a). Our results are in agreement with recent experimental work showing that *P. lapponica* fed conspecifics are more enriched in ^{15}N and ^{13}C (Asmus, 2017). Nevertheless, there are several other potential explanations for this full shift in isotopic signatures. For example, higher ^{15}N enrichment in Imnavait spiders could reflect higher consumption rates of other predatory arthropods within the food web rather than cannibalism per se, but such alternative predatory behaviours (e.g. predation on other predators) do not explain the negative association between female body size and the number of juveniles (Figure 1b). Increases in ^{15}N and ^{13}C enrichment can also occur as a result of starvation in *Pardosa* (Oelbermann & Scheu, 2002b). Thus, it is plausible that enriched isotopic signatures in wolf spiders from higher-density plots could be a reflection of starvation or nutritional stress (Adams & Sterner,

2000; Michener & Lajtha, 2008; Oelbermann & Scheu, 2002b; Webb, Hedges, & Simpson, 1998). However, given that adult body sizes are larger at Imnavait, starvation and/or nutritional stress is an unlikely explanation for enrichment of ^{15}N and ^{13}C within the entire population, because wolf spider development and body size are typically positively associated with prey quality (Oelbermann & Scheu, 2002a; Toft & Wise, 1999). Thus, we conclude that the most likely explanation for the full shift in feeding ecology is that when wolf spider densities are higher (including due to higher reproductive rates), an increase in intraspecific competition drives a forced shift in diet that includes increased cannibalism and as a result, reduces juvenile survival.

In harsh environments where growing seasons are typically short, selection for animals to consume high-quality resources that maximize growth and reproductive potential is likely to be especially strong (Elser, O'Brien, Dobberfuhl, & Dowling, 2000; Jensen, Mayntz, Toft, Raubenheimer, & Simpson, 2011). Conspecifics are suboptimal prey for wolf spiders (Asmus, 2017; Mayntz & Toft, 2006; Toft & Wise, 1999), and more frequent cannibalism among wolf spiders that are deprived of alternative prey (Petersen, Nielsen, Christensen, & Toft, 2010; Rickers & Scheu, 2005; Samu et al., 1999; Wagner & Wise, 1996) may not be advantageous for the long-term health of these populations. This is supported by our estimates of female abundance being higher at Toolik despite female body sizes being smaller (and reproductive rates being lower) there than at Imnavait (Figure 1c; Table S3). However, the population-level consequences of our findings are still unclear, because results from previous work suggest that at least in some years, total seasonal abundances of wolf spiders might be higher at Imnavait where females are larger (Rich et al., 2013). Populations of arctic arthropods are known to exhibit a high degree of interannual variability (Gillespie et al., 2019). Future studies may benefit from exploring how variation in body size and fecundity relate to long-term population viability in wolf spiders and other density-dependent species.

Understanding the consequences of body size shifts for long-term population dynamics in this dominant invertebrate predator is important, because our findings suggest that changes in wolf spider population density could potentially have cascading effects on the ecosystem. Higher rates of cannibalism among conspecifics as a result of increased reproductive rates could reduce wolf spider predation effects on lower trophic levels (Wagner & Wise, 1996). For example, detritivorous Collembola are common wolf spider prey, and these animals influence key ecosystem processes such as decomposition and nutrient cycling (Koltz, Classen, et al., 2018; Lensing & Wise, 2006). If wolf spider densities increase under climate change and as a result, cannibalism increasingly supplements wolf spider diets, then rates of spider predation on detrital prey may be dampened in the future. Whether warmer temperatures directly alter wolf spider feeding ecology as well remains unclear. Although previous work suggests that warming and increased spider densities together may induce higher rates of intraguild predation (Koltz, Classen, et al., 2018), in this study, we did not detect shifts in wolf spider diet associated with short-term warming. The context dependency of predation pressure by these

and other invertebrate consumers is an area that requires further research, particularly in rapidly changing northern ecosystems that also store a large proportion of the global pool of soil organic carbon.

In conclusion, our results demonstrate that body size variation is associated with shifts in diet and population structure within natural populations of generalist-feeding arthropod predators. These findings are a reminder that changes in body size—which is a widespread response to warmer global temperatures (Gardner et al., 2011)—may affect not only fecundity but also intraspecific competition among invertebrates. Given the complex links between different components of arthropod food webs and the important roles of these animals in ecosystem functioning, a better understanding of how rapid climate-driven shifts in body size are affecting communities and ecosystems is needed.

ACKNOWLEDGEMENTS

Funding for this research was provided by grants from the U.S. National Science Foundation (1210704), the National Geographic Committee for Research and Exploration, Conservation, Research and Education Opportunities International (CREOI), Alaska Geographic, the Kappa Delta Foundation, Lewis and Clark Fund, the Arctic Institute of North America and a Discover Denali Research Fellowship. We are grateful to Kiki Contreras, Samantha Walker and PolarTREC teachers Nick LaFave and Nell Kemp for assistance in the field, Toolik Field Station for logistical support, Shannan Sweet for providing snow data, and Gabrielle Sneed and Honey Patel for assistance in the lab. We thank Joe Bowden and two anonymous reviewers for helpful feedback on earlier drafts of this manuscript.

AUTHORS' CONTRIBUTIONS

A.M.K. conceived the ideas; A.M.K. and J.P.W. designed the methodology; A.M.K. collected and analysed the data; A.M.K. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication. The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dz08kprtz> (Koltz & Wright, 2020).

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REFERENCES

- Adams, T. S., & Sterner, R. W. (2000). The effect of dietary nitrogen content on trophic level ^{15}N enrichment. *Limnology and Oceanography*, 45, 601–607.
- Ameline, C., Høye, T. T., Bowden, J. J., Hansen, R. R., Hansen, O. L. P., Puzin, C., ... Pétilon, J. (2018). Elevational variation of body size and reproductive traits in high-latitude wolf spiders (Araneae: Lycosidae). *Polar Biology*, 41, 2561–2574.
- Asmus, A. (2017). *Arthropod food webs in Arctic tundra: trophic interactions and responses to global change*. Arlington, TX: The University of Texas.
- Balfour, R. A., Buddle, C. M., Rypstra, A. L., Walker, S. E., & Marshall, S. D. (2003). Ontogenetic shifts in competitive interactions and intra-guild predation between two wolf spider species. *Ecological Entomology*, 28, 25–30. <https://doi.org/10.1046/j.1365-2311.2002.00486.x>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.
- Belgrano, A., Allen, A. P., Enquist, B. J., & Gillooly, J. F. (2002). Allometric scaling of maximum population density: A common rule for marine phytoplankton and terrestrial plants. *Ecology Letters*, 5, 611–613. <https://doi.org/10.1046/j.1461-0248.2002.00364.x>
- Bowden, J. J., & Buddle, C. M. (2012a). Life history of tundra-dwelling wolf spiders (Araneae: Lycosidae) from the Yukon Territory, Canada. *Canadian Journal of Zoology*, 90, 714–721. <https://doi.org/10.1139/z2012-038>
- Bowden, J. J., & Buddle, C. M. (2012b). Egg sac parasitism of Arctic wolf spiders (Araneae: Lycosidae) from northwestern North America. *Journal of Arachnology*, 40, 348–350. <https://doi.org/10.1636/P11-50.1>
- Bowden, J. J., Eskildsen, A., Hansen, R. R., Olsen, K., Kurle, C. M., & Høye, T. T. (2015). High-Arctic butterflies become smaller with rising temperatures. *Biology Letters*, 11, 20150574. <https://doi.org/10.1098/rsbl.2015.0574>
- Bowden, J. J., Hansen, R. R., Olsen, K., & Høye, T. T. (2015). Habitat-specific effects of climate change on a low-mobility Arctic spider species. *Polar Biology*, 38, 559–568. <https://doi.org/10.1007/s00300-014-1622-7>
- Brose, U., Dunne, J. A., Montoya, J. M., Petchey, O. L., Schneider, F. D., & Jacob, U. (2012). Climate change in size-structured ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2903–2912. <https://doi.org/10.1098/rstb.2012.0232>
- Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., ... Cohen, J. E. (2006). Consumer–resource body-size relationships in natural food webs. *Ecology*, 87, 2411–2417. [https://doi.org/10.1890/0012-9658\(2006\)87\[2411:CBRINF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2)
- Buddle, C. M. (2000). Life history of *Pardosa moesta* and *Pardosa mackenziana* (Araneae, Lycosidae) in Central Alberta, Canada. *Journal of Arachnology*, 28, 319–328. [https://doi.org/10.1636/0161-8202\(2000\)028\[0319:LHOPMA\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2000)028[0319:LHOPMA]2.0.CO;2)
- Buddle, C. M., Walker, S. E., & Rypstra, A. L. (2003). Cannibalism and density-dependent mortality in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Canadian Journal of Zoology*, 81, 1293–1297.
- Cameron, A. C., & Trivedi, P. K. (2005). *Microeconometrics: Methods and applications*. Cambridge, UK: Cambridge University Press.
- Cameron, A. C., & Trivedi, P. K. (2013). *Regression analysis of count data*. Cambridge, UK: Cambridge University Press.
- Chamaillé-Jammes, S., Massot, M., Aragón, P., & Clobert, J. (2006). Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology*, 12, 392–402. <https://doi.org/10.1111/j.1365-2486.2005.01088.x>
- Chown, S. L., & Gaston, K. J. (2010). Body size variation in insects: A macroecological perspective. *Biological Reviews*, 85, 139–169. <https://doi.org/10.1111/j.1469-185X.2009.00097.x>
- Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 12788–12793. <https://doi.org/10.1073/pnas.0902080106>
- De Roos, A. M., Persson, L., & McCauley, E. (2003). The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters*, 6, 473–487. <https://doi.org/10.1046/j.1461-0248.2003.00458.x>
- Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., ... Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, 2, 121–124. <https://doi.org/10.1038/nclimate1347>
- Dondale, C. D. (1961). Life histories of some common spiders from trees and shrubs in Nova Scotia. *Canadian Journal of Zoology*, 39, 777–787. <https://doi.org/10.1139/z61-074>

- Dondale, C., & Redner, J. (1990). *The wolf spiders, nursery web spiders, and lynx spiders of Canada and Alaska: Araneae: Lycosidae, Pisauridae and Oxyopidae. Insects and arachnids of Canada handbook*. Ottawa, ON: Agriculture Canada.
- Elser, J., O'Brien, W., Dobberfuhl, D., & Dowling, T. (2000). The evolution of ecosystem processes: Growth rate and elemental stoichiometry of a key herbivore in temperate and arctic habitats. *Journal of Evolutionary Biology*, 13, 845–853. <https://doi.org/10.1046/j.1420-9101.2000.00215.x>
- Fox, C. W., & Czesak, M. E. (2000). Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology*, 45, 341–369. <https://doi.org/10.1146/annurev.ento.45.1.341>
- Fox, L. R. (1975). Cannibalism in natural populations. *Annual Review of Ecology and Systematics*, 6, 87–106. <https://doi.org/10.1146/annurev.es.06.110175.000511>
- Gardner, J. L., Peters, A., Kearney, M. R., Joseph, L., & Heinsohn, R. (2011). Declining body size: A third universal response to warming? *Trends in Ecology & Evolution*, 26, 285–291. <https://doi.org/10.1016/j.tree.2011.03.005>
- Gillespie, M. A. K., Alfredsson, M., Barrio, I. C., Bowden, J. J., Convey, P., Culler, L. E., ... Høye, T. T. (2019). Status and trends of terrestrial arthropod abundance and diversity in the North Atlantic region of the Arctic. *Ambio*, 49(3), 718–731. <https://doi.org/10.1007/s13280-019-01162-5>
- Gough, L. (2012). Abundance of major taxonomic groups of invertebrates (arthropods and gastropods) collected with pitfall traps at four sites near Toolik Field Station Arctic LTER, Alaska in the summer of 2010. Environmental Data Initiative.
- Hagstrum, D. W. (1971). Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and the field. *Annals of the Entomological Society of America*, 64, 757–760.
- Honěk, A., & Honek, A. (1993). Intraspecific variation in body size and fecundity in insects: A general relationship. *Oikos*, 66, 483–492. <https://doi.org/10.2307/3544943>
- Høye, T. T., & Forchhammer, M. C. (2008a). The influence of weather conditions on the activity of high-arctic arthropods inferred from long-term observations. *BMC Ecology*, 8, 8. <https://doi.org/10.1186/1472-6785-8-8>
- Høye, T. T., & Forchhammer, M. C. (2008b). Phenology of high-arctic arthropods: Effects of climate on spatial, seasonal, and inter-annual variation. *Advances in Ecological Research*, 40, 299–324.
- Høye, T. T., & Hammel, J. U. (2010). Climate change and altitudinal variation in sexual size dimorphism of arctic wolf spiders. *Climate Research*, 41, 259–265. <https://doi.org/10.3354/cr00855>
- Høye, T. T., Hammel, J. U., Fuchs, T., & Toft, S. (2009). Climate change and sexual size dimorphism in an Arctic spider. *Biology Letters*, 5, 542–544. <https://doi.org/10.1098/rsbl.2009.0169>
- Jensen, K., Mayntz, D., Toft, S., Raubenheimer, D., & Simpson, S. J. (2011). Nutrient regulation in a predator, the wolf spider *Pardosa prativaga*. *Animal Behaviour*, 81, 993–999. <https://doi.org/10.1016/j.anbehav.2011.01.035>
- Kalinkat, G., Jochum, M., Brose, U., & Dell, A. I. (2015). Body size and the behavioral ecology of insects: Linking individuals to ecological communities. *Current Opinion in Insect Science*, 9, 24–30. <https://doi.org/10.1016/j.cois.2015.04.017>
- Kalinkat, G., Schneider, F. D., Digel, C., Guill, C., Rall, B. C., & Brose, U. (2013). Body masses, functional responses and predator-prey stability. *Ecology Letters*, 16, 1126–1134. <https://doi.org/10.1111/ele.12147>
- Koltz, A. M., Asmus, A., Gough, L., Pressler, Y., & Moore, J. C. (2018). The detritus-based microbial-invertebrate food web contributes disproportionately to carbon and nitrogen cycling in the Arctic. *Polar Biology*, 41, 1531–1545. <https://doi.org/10.1007/s00300-017-2201-5>
- Koltz, A. M., Classen, A. T., & Wright, J. P. (2018). Warming reverses top-down effects of predators on belowground ecosystem function in Arctic tundra. *Proceedings of the National Academy of Sciences of the United States of America*, 115, E7541–E7549. <https://doi.org/10.1073/pnas.1808754115>
- Koltz, A. M., & Wright, J. P. (2020). Data from: Impacts of female body size on cannibalism and juvenile abundance in a dominant arctic spider. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.dz08kprtz>
- Kruse, P. D., Toft, S., & Sunderland, K. D. (2008). Temperature and prey capture: Opposite relationships in two predator taxa. *Ecological Entomology*, 33, 305–312. <https://doi.org/10.1111/j.1365-2311.2007.00978.x>
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82, 1–26.
- Legault, G., & Weis, A. E. (2013). The impact of snow accumulation on a heath spider community in a sub-Arctic landscape. *Polar Biology*, 36, 885–894. <https://doi.org/10.1007/s00300-013-1313-9>
- Lensing, J. R., & Wise, D. H. (2006). Predicted climate change alters the indirect effect of predators on an ecosystem process. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 15502–15505. <https://doi.org/10.1073/pnas.0607064103>
- Marshall, S. D., & Gittleman, J. L. (1994). Clutch size in spiders: Is more better? *Functional Ecology*, 8, 118–124. <https://doi.org/10.2307/2390120>
- Mayntz, D., & Toft, S. (2006). Nutritional value of cannibalism and the role of starvation and nutrient imbalance for cannibalistic tendencies in a generalist predator. *Journal of Animal Ecology*, 75, 288–297. <https://doi.org/10.1111/j.1365-2656.2006.01046.x>
- Michener, R., & Lajtha, K. (2008). *Stable isotopes in ecology and environmental science* (2nd ed.). Boston, MA: Blackwell Publishers.
- Mullahy, J. (1986). Specification and testing of some modified count data models. *Journal of Econometrics*, 33, 341–365. [https://doi.org/10.1016/0304-4076\(86\)90002-3](https://doi.org/10.1016/0304-4076(86)90002-3)
- Nisbet, R., & Onyiah, L. (1994). Population dynamic consequences of competition within and between age classes. *Journal of Mathematical Biology*, 32, 329–344. <https://doi.org/10.1007/BF00160164>
- Oelbermann, K., & Scheu, S. (2002a). Effects of prey type and mixed diets on survival, growth and development of a generalist predator, *Pardosa lugubris* (Araneae: Lycosidae). *Basic and Applied Ecology*, 3, 285–291.
- Oelbermann, K., & Scheu, S. (2002b). Stable isotope enrichment ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) in a generalist predator (*Pardosa lugubris*, Araneae: Lycosidae): Effects of prey quality. *Oecologia*, 130, 337–344.
- Overland, J., Hanna, E., Hanssen-Bauer, I., Kim, S., Walsh, J., Wang, M., ... Thoman, R. (2017). Surface air temperature [in Arctic Report Card 2017]. NOAA Arctic Program.
- Persson, L., & de Roos, A. M. (2013). Symmetry breaking in ecological systems through different energy efficiencies of juveniles and adults. *Ecology*, 94, 1487–1498. <https://doi.org/10.1890/12-1883.1>
- Petersen, A., Nielsen, K. T., Christensen, C. B., & Toft, S. (2010). The advantage of starving: Success in cannibalistic encounters among wolf spiders. *Behavioral Ecology*, 21, 1112–1117. <https://doi.org/10.1093/beheco/arq119>
- Pickavance, J. R. (2001). Life-cycles of four species of *Pardosa* (Araneae, Lycosidae) from the island of Newfoundland, Canada. *Journal of Arachnology*, 29, 367–377. [https://doi.org/10.1636/0161-8202\(2001\)029\[0367:LCOFSO\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2001)029[0367:LCOFSO]2.0.CO;2)
- Polis, G. (1988). Exploitation competition and the evolution of interference, cannibalism, and intraguild predation in age/size-structured populations. In B. Ebenman & L. Persson (Eds.), *Size-structured populations* (pp. 185–202). Berlin, Germany: Springer.
- Ponsard, S., & Arditi, R. (2000). What can stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) tell about the food web of soil macro-invertebrates? *Ecology*, 81, 852–864.
- Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83, 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)

- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reed, D. H., & Nicholas, A. C. (2008). Spatial and temporal variation in a suite of life-history traits in two species of wolf spider. *Ecological Entomology*, 33, 488–496. <https://doi.org/10.1111/j.1365-2311.2008.00994.x>
- Rich, M. E., Gough, L., & Boelman, N. T. (2013). Arctic arthropod assemblages in habitats of differing shrub dominance. *Ecography*, 36, 994–1003. <https://doi.org/10.1111/j.1600-0587.2012.00078.x>
- Rickers, S., Langel, R., & Scheu, S. (2006). Stable isotope analyses document intraguild predation in wolf spiders (Araneae: Lycosidae) and underline beneficial effects of alternative prey and microhabitat structure on intraguild prey survival. *Oikos*, 114, 471–478. <https://doi.org/10.1111/j.2006.0030-1299.14421.x>
- Rickers, S., & Scheu, S. (2005). Cannibalism in *Pardosa palustris* (Araneae, Lycosidae): Effects of alternative prey, habitat structure, and density. *Basic and Applied Ecology*, 6, 471–478. <https://doi.org/10.1016/j.baae.2005.02.007>
- Rypstra, A. L., & Samu, F. (2005). Size dependent intraguild predation and cannibalism in coexisting wolf spiders (Araneae, Lycosidae). *The Journal of Arachnology*, 33, 390–398. <https://doi.org/10.1636/CT05-10.1>
- Sackett, T. E., Buddle, C. M., & Vincent, C. (2008). Relevance of collected juveniles to the analysis of spider communities. *The Journal of Arachnology*, 36, 187–191. <https://doi.org/10.1636/T07-51SC.1>
- Samu, F., Toft, S., & Kiss, B. (1999). Factors influencing cannibalism in the wolf spider *Pardosa agrestis* (Araneae, Lycosidae). *Behavioral Ecology and Sociobiology*, 45, 349–354. <https://doi.org/10.1007/s002650050570>
- Sanders, D., Vogel, E., & Knop, E. (2015). Individual and species-specific traits explain niche size and functional role in spiders as generalist predators. *Journal of Animal Ecology*, 84, 134–142. <https://doi.org/10.1111/1365-2656.12271>
- Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., & Charnov, E. L. (2004). Effects of body size and temperature on population growth. *The American Naturalist*, 163, 429–441. <https://doi.org/10.1086/381872>
- Sim, K. A., Buddle, C. M., & Wheeler, T. A. (2014). Species boundaries of *Pardosa concinna* and *P. lapponica* (Araneae: Lycosidae) in the northern Nearctic: Morphology and DNA barcodes. *Zootaxa*, 3884(2), 169–178. <https://doi.org/10.11646/zootaxa.3884.2.5>
- Simpson, M. R. (1993). Reproduction in two species of arctic arachnids, *Pardosa glacialis* and *Alopecosa hirtipes*. *Canadian Journal of Zoology*, 71, 451–457.
- Sticht, C., Schrader, S., & Giesemann, A. (2006). Influence of chemical agents commonly used for soil fauna investigations on the stable C-isotopic signature of soil animals. *European Journal of Soil Biology*, 42, S326–S330.
- Sweet, S. K., Gough, L., Griffin, K. L., & Boelman, N. T. (2014). Tall deciduous shrubs offset delayed start of growing season through rapid leaf development in the Alaskan Arctic Tundra. *Arctic, Antarctic, and Alpine Research*, 46, 682–697. <https://doi.org/10.1657/1938-4246-46.3.682>
- Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., & Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, 23, GB2023. <https://doi.org/10.1029/2008GB003327>
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535, 241–245. <https://doi.org/10.1038/nature18608>
- Toft, S., & Wise, D. H. (1999). Growth, development and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia*, 119, 191–197. <https://doi.org/10.1007/s004420050776>
- Wagner, J. D., & Wise, D. H. (1996). Cannibalism regulates densities of young wolf spiders: Evidence from field and laboratory experiments. *Ecology*, 77, 639–652. <https://doi.org/10.2307/2265637>
- Warren, R., Price, J., Graham, E., Forstenhaeusler, N., & VanDerWal, J. (2018). The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5 C rather than 2 C. *Science*, 360, 791–795.
- Webb, S. C., Hedges, R., & Simpson, S. J. (1998). Diet quality influences the ^{13}C and ^{15}N of locusts and their biochemical components. *Journal of Experimental Biology*, 201, 2903–2911.
- Wise, D. H. (2004). Wandering spiders limit densities of a major micro-bi-detritivore in the forest-floor food web. *Pedobiologia*, 48, 181–188. <https://doi.org/10.1016/j.pedobi.2003.12.001>
- Wise, D. H. (2006). Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. *Annual Review of Entomology*, 51, 441–465. <https://doi.org/10.1146/annurev.ento.51.110104.150947>
- Wise, D. H., Moldenhauer, D. M., & Halaj, J. (2006). Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecological Applications*, 16, 865–876. [https://doi.org/10.1890/1051-0761\(2006\)016\[0865:USITRS\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[0865:USITRS]2.0.CO;2)
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology & Evolution*, 20, 402–409. <https://doi.org/10.1016/j.tree.2005.04.005>
- Wyant, K. A., Draney, M. L., & Moore, J. C. (2011). Epigeal spider (Araneae) communities in moist acidic and dry heath tundra at Toolik Lake, Alaska. *Arctic, Antarctic, and Alpine Research*, 43, 301–312. <https://doi.org/10.1657/1938-4246-43.2.301>
- Zeileis, A., Kleiber, C., & Jackman, S. (2008). Regression models for count data in R. *Journal of Statistical Software*, 27, 1–25.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Koltz AM, Wright JP. Impacts of female body size on cannibalism and juvenile abundance in a dominant arctic spider. *J Anim Ecol*. 2020;89:1788–1798. <https://doi.org/10.1111/1365-2656.13230>