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Susan E. Anthony
Western University, santho2@uwo.ca

Christopher M. Buddle
McGill University

Toke T. Høye
Aarhus University

Brent J. Sinclair
Western University, bsincla7@uwo.ca

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1 **Thermal limits of summer-collected *Pardosa* wolf spiders (Araneae: Lycosidae) from the**
2 **Yukon Territory and Greenland**

3
4 Susan E. Anthony^{1*}, Christopher M. Buddle², Toke T. Høye³ & Brent J Sinclair¹

5
6 ¹Department of Biology, University of Western Ontario, London, ON, Canada

7 ²Department of Natural Resource Sciences, McGill University, Macdonald Campus, Ste-Anne-
8 de-Bellevue, QC, Canada

9 ³Department of Bioscience, Arctic Research Centre, Grenåvej 14, 8410 Rønne, Aarhus
10 University, Denmark

11 *Author for correspondence: Susan Anthony, Department of Biology, University of
12 Western Ontario, 1151 Richmond St. N, London, ON, N6A 5B7, Canada

13 Email santho2@uwo.ca; Tel. +1-519-661-2111 x 89158; Fax +1-519-661-3935

14

15 Susan E. Anthony OrcID: 0000-0003-1533-1817

16 Christopher M. Buddle OrcID: 0000-0002-7494-9732

17 Toke T. Høye OrcID: 0000-0001-5387-3284

18 Brent J. Sinclair OrcID: 0000-0002-8191-9910

19

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22 **Abstract**

23 Arctic and sub-Arctic terrestrial ectotherms contend with large daily and seasonal temperature
24 ranges. However, there are few data available on the thermal biology of these high latitude
25 species, especially arachnids. We determined the lower and upper thermal limits of seven species
26 of wolf spider from the genus *Pardosa* (Araneae: Lycosidae) collected in summer from the
27 Yukon Territory (Canada) and Southern Greenland. None of these species survived freezing, and
28 while spiderlings appeared freeze-avoidant, surviving to their supercooling point (SCP, the
29 temperature at which they spontaneously freeze), chill-susceptible adults and juveniles died at
30 temperatures above their SCP. The critical thermal minimum (CT_{min} , the lower temperature of
31 activity) and SCP were very close (spiders continued moving until they freeze), and at -5.4 to -
32 8.4 °C, are not substantially lower than those of lower latitude species. The SCP of spiderlings
33 was significantly lower than that of overwintering juveniles or adults, likely because of their
34 small size. There was no systematic variation in SCP among collection sites, latitude, or species.
35 Critical thermal maxima (CT_{max}) ranged from 42.3 to 46.8 °C, showed no systematic patterns of
36 variation, and were also similar to those of lower-latitude relatives. Overall, heat tolerances of
37 the *Pardosa* spp. were likely sufficient to tolerate even very warm Arctic summer temperatures,
38 but cold tolerance is probably inadequate to survive winter conditions. We expect that seasonal
39 thermal plasticity is necessary for overwintering in these species.

40

41 **Key Words:**

42 Ectotherm, supercooling point, CT_{max} , CT_{min} , *Pardosa*, critical thermal limits

43 **Introduction**

44 Terrestrial ectotherms in the Arctic experience substantial seasonal temperature fluctuations. For
45 example, air temperature extremes in Eagle Plains, Yukon, Canada (66.4°N) between 2010 and
46 2016 ranged from +30.4 °C in the summer to -39.7 °C in the winter (Road Weather Information
47 System [RWIS], Government of Yukon). Mean temperatures in the Arctic are expected to
48 increase by as much as 9 °C as a result of climate change (IPCC 2014), with additional impacts
49 from predicted increases in the frequency of extreme weather events (Post et al. 2009; IPCC
50 2014). The altered Arctic climate has already resulted in changes in ectotherm body size (Høye
51 et al. 2009; Bowden et al. 2013, 2015a) and distribution (Parmesan et al. 1999; Jepsen et al.
52 2011); as well as phenological mismatch between herbivorous insects and their host plants (Høye
53 and Forchhammer 2008; Post and Forchhammer 2008).

54 The need to predict the responses of terrestrial ectotherms to climate change has
55 motivated a range of macrophysiological studies relating environmental conditions to thermal
56 performance and fitness (Deutsch et al. 2008; Sunday et al. 2011; Sinclair et al. 2016; Bennett et
57 al. 2018). A key conclusion of this work has been that tropical ectotherms are more vulnerable
58 to climate change than their polar counterparts. However, these macrophysiological studies are
59 dependent on the quality of input data and often include only a limited Arctic dataset. For
60 example, Deutsch et al. (2008) exclude locations beyond 60°N and 60°S, while Sunday et al.
61 (2011) include only marine organisms north of 60°N. Thus, these ‘global-scale’ conclusions (and
62 resultant policy decisions) are drawn without reference to terrestrial Arctic arthropods. Holarctic
63 spiders are speciose (Marusik and Koponen 2005) abundant (Coulson 2000), and subject to long-
64 term monitoring (Gillespie et al. 2019), which means that, if thermal biology data were available,
65 they would be ideal for inclusion in these macrophysiological analyses.

66 The cosmopolitan wolf spider genus *Pardosa* (Lycosidae) reaches high densities in the
67 Arctic and sub-Arctic; for example, there are 3.4 individuals·m⁻² in the Ogilvie Mountain area of
68 the Yukon Territory (Turney et al. 2018). At high latitudes, *Pardosa* emerge as juveniles in late
69 spring to feed and grow; older individuals mature into adults, while others overwinter again as
70 juveniles (Buddle 2000; Pickavance 2001). After mating, the females produce one or two egg
71 sacs per summer. These high-latitude *Pardosa* will encounter both high and low temperatures
72 during the summer growth and reproductive season (e.g., in Narsarsuaq, Greenland, on June 21,
73 2016, the temperature ranged from +2.1 to +20.4 °C within 24 h; TTH, unpublished data).
74 Because of their abundance and ecological importance, and the extensive documentation of their
75 responses to climate change (e.g. Høye et al. 2009), Arctic *Pardosa* are an appropriate target
76 taxon for broadening our understanding of the thermal biology of polar spiders.

77 In ectotherms, activity is temperature-dependent, bounded by the critical thermal
78 minimum (CT_{\min}) and maximum (CT_{\max}), the temperatures at which the ectotherm can no longer
79 move (Huey and Kingsolver 1989; Sinclair et al. 2016). Critical thermal limits vary among both
80 species and populations (Sinclair et al. 2012); in many cases, arthropods living at higher latitudes
81 have broader thermal tolerances (measured as the range between CT_{\min} and CT_{\max}), presumably
82 reflecting a latitudinal increase in temperature variance (Calosi et al. 2010). Generally, this
83 broadening thermal tolerance range is driven by greater cold tolerance (Addo-Bediako et al.
84 2000). The CT_{\min} of spiders can range as low as -8 °C in the sub-Antarctic linyphiid *Prinerigone*
85 *vagans* (Jumbam et al. 2008). The only CT_{\min} reported for a lycosid is -2.3 °C in *Pardosa*
86 *groenlandica* (Lycosidae) from 44.6°N in Nova Scotia, Canada (Murphy et al. 2008), although
87 Bayram and Luff (1993a) suggest an activity threshold (which is probably close to the CT_{\min}) of
88 2°C for *Pardosa pullata* in northern England. The CT_{\max} of subadult *Pardosa nigriceps* from

89 Southern Sweden (55.4°N) was +39.7 °C (Almquist 1970), and *Rabidosa rabida* from Arkansas,
90 USA (34.7°N) is +42.9 °C (Stork 2012). In temperate riparian lycosids, microhabitat distribution
91 is determined by a combination of high temperature and desiccation tolerance (DeVito et al.
92 2004), suggesting that upper thermal limits are ecologically relevant, at least in hot
93 environments.

94 Below the CT_{\min} , arthropods use two main strategies to survive low temperatures: freeze-
95 tolerance and freeze-avoidance. Freeze-tolerant species can survive internal ice formation
96 (Sinclair et al. 2015), whereas freeze-avoidant species are killed by ice formation at their
97 supercooling point (SCP), the temperature at which they freeze, however they will survive low
98 temperatures if unfrozen (Sinclair et al. 2015). By contrast, chill-susceptible species die from low
99 temperatures unrelated to freezing. Spiders that have been studied have been chill-susceptible
100 (Kirchner 1973) or freeze-avoidant (Lee and Baust 1985). Stork (2012) reports that *Rabidosa*
101 *rabida* did not survive freezing, implying that it is either freeze-avoidant or chill-susceptible, and
102 Bayram and Luff (1993b) report mortality of *Pardosa pullata* at temperatures above the SCP,
103 implying chill-susceptibility.

104 Although the ecology of Arctic spiders has received some attention (Hodkinson et al.
105 2001; Bowden and Buddle 2012; Bowden et al. 2015b; Høye and Culler 2018), there is relatively
106 little information about their thermal biology. This lack of data could account for the absence of
107 polar spiders from macrophysiological studies, in spite of their ecological importance and
108 susceptibility to climate change in the Arctic. Here we report the SCP, cold tolerance strategy,
109 CT_{\min} , and CT_{\max} of seven species of *Pardosa* wolf spiders collected from sub-Arctic and Arctic
110 (c. 61°N - 70°N) habitats in the Yukon Territory (Canada) and Greenland (c. 61°N - 70°N),
111 contributing to the data available to study global patterns of ectotherm thermal biology.

112 **Materials and Methods**

113 *Animal collections*

114 We studied seven species of *Pardosa* that could be readily collected at our field sites
115 (Table 1). All of these species overwinter for one or more years as juveniles, with adults present
116 and reproducing only in the spring (Pickavance 2001). Of these species, *P. furcifera*, *P. glacialis*,
117 *P. groenlandica*, *P. hyperborea*, *P. lapponica*, and *P. sodalis* are found only at high latitudes,
118 while *P. moesta* is distributed from the Arctic to more temperate latitudes (Utah and Tennessee)
119 in North America (Dondale and Redner, 1987).

120 We collected active *Pardosa* spiders by hand into 30-mL plastic containers at nine
121 locations during the boreal summers of 2015 and 2016 (Table 1). Because of the timing of
122 collections, a majority of spiders we collected were female or juvenile (see Table 1); males were
123 included in our analyses only where sample size allowed. We collected adult *P. lapponica*, *P.*
124 *sodalis*, *P. glacialis*, and *P. moesta* from tundra in Yukon Territory (Yukon Science and
125 Explorer's License 15-15S&E) at three sites along the Dempster Highway, between July 2 and
126 July 10, 2015 (Table 1). The Yukon sites were mostly moist tundra, dominated by low-lying
127 vegetation, with the exception of *P. glacialis*, which we collected from a scree field at the
128 Yukon-North West Territories border (YT-NWT). We maintained the spiders in their collection
129 containers, with damp moss and food (one flightless *Drosophila melanogaster* given every two
130 to three days) and returned them in insulated containers to Western University in London, ON,
131 where they were housed at 12 °C under 24 h light, mimicking Northern Yukon summer
132 conditions. We made all measurements between 4 and 17 days of collection.

133 We collected *P. furcifera*, *P. groenlandica*, and *P. hyperborea* within a two-hour walk of
134 Narsarsuaq in Southern Greenland (Table 1) between June 21 and August 2, 2016 (Greenland

135 Survey License G16-042). Lowland sites were from sea level to c. 80 m a.s.l. and included rocky
136 cobble riverbed (*P. groenlandica*), and moss- and lichen-dominated fen (*P. furcifera* and *P.*
137 *hyperborea*). Air temperatures during the collection period (1.5 m above ground) ranged from 2
138 to 22 °C (using a HOBO U30-NRC Weather Station, Onset Computer Corporation, Bourne,
139 MA). The high elevation site was c. 450 m a.s.l. and the *P. furcifera* and *P. hyperborea* habitat
140 was similar to the low elevation site, albeit drier and windier, whereas we collected *P.*
141 *groenlandica* from dried lake beds. After returning to the laboratory in Narsarsuaq, we held the
142 animals in their collection containers in a clear plastic container in a shaded outdoor area. We
143 separated the Narsarsuaq-collected spiders by age and sex (spiderling, juvenile, sexually mature
144 female, sexually mature male); with the exception of the spiderlings, which were still carried on
145 their mother's abdomen (n=3 *P. hyperborea* mothers; n=4 *P. groenlandica* mothers), until we
146 removed them with a paintbrush immediately before the experiments. We measured thermal
147 limits of the Narsarsuaq-collected *Pardosa* within three days of collection; we did not feed them
148 during that period.

149 Adult female *Pardosa glacialis* were collected by hand at two sites on Disko Island, West
150 Greenland (Table 1): at low elevation (50 m a.s.l.) in Blæsedalen, and in a nearby areas with hot
151 springs (50 m a.s.l.) with constant stream temperatures around 10°C. The low elevation site was
152 in dry heath vegetation dominated by *Dryas integrifolia* and *Cassiope tetragona*. The areas
153 surrounding the hot springs were moss dominated. The summer temperatures at Disko Island are
154 about 5 °C cooler than at the collection sites in Narsarsuaq (DMI Is Centralen, www.dmi.dk).
155 The spiders were shipped from Disko Island to Narsarsuaq in 3-mL plastic tubes and kept moist
156 with water-soaked cotton wool. We did not feed the Disko spiders and measured thermal limits
157 approximately one week after collection.

158

159 *Measurements of Thermal Biology*

160 We measured SCP by putting the spiders in 1.7-mL microcentrifuge tubes in contact with
161 a 36-AWG type-T copper-constantan thermocouple (OMEGA, Laval, Quebec, Canada), held in
162 place with cotton wool. We recorded temperature every 0.5 s using a TC-08 interface and
163 PicoLog software (Pico Technology, Cambridge, UK). The tubes containing the Yukon-collected
164 spiders were placed in holes milled in metal blocks cooled from 12 °C at 0.1 °C·min⁻¹ by a
165 refrigerated 50% methanol blend (Lauda Proline 3530, Würzburg, Germany) (Sinclair et al.
166 2015). We cooled the Greenland-collected spiders from 15 °C to 0 °C, at -1.0 °C·min⁻¹, then at -
167 0.5 °C·min⁻¹ in a custom-built Peltier-effect cooled copper block. SCP was defined as the lowest
168 temperature immediately before the exotherm (Sinclair et al. 2015). We determined the cold
169 tolerance strategy as outlined by Sinclair et al. (2015). Dead individuals were those that did not
170 move or right themselves 24 h post-chill. For SCP determination of spiderlings, we attached the
171 spiders to the thermocouple using silicone vacuum grease; because it is hard to remove the
172 spiderlings from the grease without damaging them, we did not formally determine their cold
173 tolerance strategy.

174 We measured CT_{\min} by cooling the animals using an approach described by Sinclair et al.
175 (2015). For Yukon-collected spiders, we used jacketed glass chambers cooled by 50% ethylene
176 glycol flowing from a refrigerated circulator (Model 1157P, VWR International, Mississauga,
177 ON, Canada) as described by MacMillan and Sinclair (2011). For Greenland-collected spiders,
178 we housed the spiders in a custom-built copper arena with temperature controlled by a Peltier-
179 effect device. In both cases, we monitored the chamber temperatures with a 36-AWG type-T
180 copper-constantan thermocouple (OMEGA, Laval, Quebec, Canada) connected to a TC-08

181 interface and PicoLog software (Pico Technology, Cambridge, UK). We cooled the Greenland-
182 collected spiders from 15 °C to 0 °C at 1.0 °C·min⁻¹, followed by 0.25 °C·min⁻¹ until they
183 reached their CT_{\min} ; we cooled the Yukon spiders starting at 12 °C by 0.25°C·min⁻¹. We
184 determined CT_{\min} as the temperature at which the animals no longer responded to touch from a
185 paintbrush, and their legs curled without apparent control (Sinclair et al. 2015). We observed that
186 adult low elevation *P. groenlandica* and *P. furcifera* responded to touch until they froze at their
187 SCP (SEA, *pers. obs.*), suggesting that the CT_{\min} and SCP coincided, allowing us to measure
188 SCP as a proxy for lower lethal temperature in these cases.

189 To determine CT_{\max} , we heated the spiders in the apparatus previously described for
190 cooling. We warmed the Greenland-collected spiders at 1.0 °C·min⁻¹ from 15 °C to 30 °C, then
191 +0.25 °C·min⁻¹ above 30 °C, and the Yukon-collected spiders at 0.25 °C·min⁻¹ from 12 °C until
192 the animals spasmed, and their legs curled (Lutterschmidt and Hutchison 1997). We weighed the
193 *Pardosa* spiders after the measurements of thermal tolerance.

194

195 *Analyses*

196 We compared the SCP and CT_{\max} within *Pardosa* species among age group (spiderling,
197 juvenile, and adult females), elevation (high and low), and the age × elevation interaction by 2-
198 way ANOVA and Tukey's *post hoc* test. We tested the interaction between juveniles and adults
199 because they may respond differently to their microclimates separated by elevation. Where
200 sufficient males were available to measure a trait, we compared adult males and females using
201 Welch's t-test. We compared the CT_{\max} in *P. lapponica* and *P. sodalis* between populations
202 separated by latitude in the Yukon by Welch's t-test; we did not collect sufficient *Pardosa* from
203 each collection site in the Yukon to allow latitudinal comparisons within species of SCP and

204 CT_{\min} , nor were there enough species to test for correlation between mean body size and mean
205 SCP or CT_{\max} among species. We performed all analyses using R version 3.2.2 (R Development
206 Core Team, 2016). All raw data are available in the supplementary online material.

207 **Results**

208 None of the 275 spiders we froze as part of SCP or cold tolerance strategy determinations
209 survived ice formation. Cold tolerance strategies are summarized in Table 2. All juvenile spiders
210 we measured were freeze avoidant, as were all adult females from the Yukon and adult female *P.*
211 *furcifera* and *P. groenlandica* from high elevations in Greenland. Adult female *P. groenlandica*
212 from low elevation were chill-susceptible, as were all the *P. hyperborea* adult females. *Pardosa*
213 *groenlandica* (high and low elevation) and *P. hyperborea* spiderlings appeared to be chill-
214 susceptible, however, much mortality was likely due to the difficulty of removing the spiders
215 from the adhering grease, making it difficult to separate handling- and cold-related mortality.

216 The SCPs of Arctic *Pardosa* ranged from -23.3 °C in a low elevation *P. groenlandica*
217 spiderling, to -4.5 °C in two *P. glacialis* adult females collected at near hot springs on Disko
218 Island, Greenland. The mean SCPs of Yukon-collected *Pardosa* ranged from -5.4 °C ± 0.2 ($n =$
219 10; female *P. lapponica*) to -6.8 °C ± 0.3 ($n = 8$; female *P. glacialis*), and in adult Yukon
220 females, the SCP appears to be slightly higher in larger species (Fig. 2). Among *P. glacialis*, the
221 SCP of the low elevation Disko Island population was significantly higher than both the hot
222 springs location and those collected from the Yukon Territory (Table 3, 4).

223 Within the Greenland-collected species, the SCP of *P. furcifera* juveniles was
224 significantly lower than that of the adult females ($F_{2,32} = 5.46, p = 0.009$), however there was no
225 effect of elevation on SCP nor an age × elevation interaction (Table 3, 4). *Pardosa groenlandica*
226 and *P. hyperborea* spiderlings had lower mean SCPs than juveniles and adult females of the
227 same species; the SCP of the *P. groenlandica* spiderlings was higher in the high elevation site,
228 and there was an age × elevation interaction (Table 3, 4). Eliminating the spiderlings from the
229 analysis, the SCP of *P. groenlandica* and *P. hyperborea* juveniles and adult females did not

230 differ, nor was there a difference in SCP between collection elevations, or an age \times elevation
231 interaction (Table 3). The SCPs of adult male and female *P. furcifera* (low elevation), *P.*
232 *groenlandica* (high elevation), and *P. hyperborea* (low elevation) did not differ significantly
233 (Table 3, 4).

234 The lowest CT_{\min} we measured was $-6.9\text{ }^{\circ}\text{C}$ in an adult female *P. glacialis* from the YT-
235 NWT Border, while the highest was $+1.7\text{ }^{\circ}\text{C}$ in an adult female *P. lapponica* from Tombstone
236 Mountains in the Yukon Territory. The mean CT_{\min} of the Yukon-collected *Pardosa* fell within a
237 $1.4\text{ }^{\circ}\text{C}$ range; from $-4.5 \pm 0.3\text{ }^{\circ}\text{C}$ ($n = 9$; adult female *P. moesta*) to $-5.7 \pm 0.3\text{ }^{\circ}\text{C}$ ($n = 10$; adult
238 female *P. glacialis*; Fig. 1), and there was no difference in CT_{\min} among the Yukon-collected
239 *Pardosa* species (Fig. 1). The CT_{\min} of the juvenile, Greenland-collected *P. groenlandica* from
240 low elevations was $-2.2 \pm 0.2\text{ }^{\circ}\text{C}$ ($n = 11$; Fig. 1).

241 The CT_{\max} of Arctic *Pardosa* ranged from $+30.5\text{ }^{\circ}\text{C}$ in an adult female *P. lapponica* from
242 the YT-NWT border, to $+48.7\text{ }^{\circ}\text{C}$ in an adult female *P. glacialis* from the Ogilvie Mountains.
243 The mean CT_{\max} of Greenland-collected *Pardosa* fell between $42.3 \pm 0.3\text{ }^{\circ}\text{C}$ ($n = 10$) and $46.6\text{ }^{\circ}\text{C}$
244 $\pm 0.5\text{ }^{\circ}\text{C}$ ($n = 11$), and CT_{\max} was generally higher in larger species (Table 5).

245 Within species, there was no relationship between CT_{\max} and latitude within the Yukon-
246 collected *P. lapponica* and *P. sodalis* (*P. lapponica*: $t_{4.8} = 0.788$, $p = 0.468$; *P. sodalis*: $t_{4.7} =$
247 0.681 , $p = 0.528$; Table 5). Within the Greenland-collected *Pardosa*, the CT_{\max} of juvenile *P.*
248 *furcifera* was significantly lower than female adults, but there was no difference between the
249 high and low elevation populations (Table 3, 5). The CT_{\max} was higher in the juvenile *P.*
250 *hyperborea* than the female adults: the CT_{\max} of all *P. hyperborea* from higher elevation
251 populations were significantly lower than that of spiders from lower elevations. There was also
252 an age \times elevation interaction: the juveniles had a greater increase in CT_{\max} between populations

253 than the female adults (Table 3, 5). The CT_{\max} of *P. glacialis* collected from the Yukon was
254 similar to that of the Disko Island hot spring population, and they were both c. 2 °C higher than
255 that of the Disko Island low elevation population ($F_{2,32} = 31.56, p < 0.001$; Table 5).

256

257 **Discussion**

258 Spiders are abundant in Arctic and sub-Arctic terrestrial ecosystems (Hodkinson et al.
259 2001), yet because their thermal biology has received only limited attention they are poorly
260 represented in global-scale meta-analyses (e.g., Deutsch et al. 2008; Sunday et al. 2011). Here,
261 we show that the CT_{\min} and SCP of *Pardosa* from Greenland and Yukon are slightly lower than
262 those of their lower-latitude congeners: c. 3 °C lower than *P. groenlandica* collected in Nova
263 Scotia, Canada (Murphy et al. 2008) and both summer- and winter-collected *Pardosa* from
264 Northern England (Bayram and Luff 1993b). By contrast, their CT_{\max} is similar to that of lower-
265 latitude spiders (e.g. Schmalhofer 1999). This pattern is consistent with observations for insects
266 (Addo-Bediako et al. 2000), in which species are more cold-tolerant towards the poles, but there
267 is little latitudinal variation in upper thermal limits.

268 In keeping with reports for other spiders (Kirchner 1973; Kirchner 1987), we found that
269 summer-collected Greenland and Yukon *Pardosa* were largely chill-susceptible. We note that in
270 almost all cases, the CT_{\min} and SCP appeared to be very close together. For example, the freeze-
271 avoidant Yukon-collected adult female *P. lapponica* has a mean CT_{\min} of -5.5 °C and a mean
272 SCP of -5.4 °C (Fig 1). We use the proximity of CT_{\min} , SCP, and lethal temperature to justify
273 using SCP as a convenient metric of cold tolerance in these species. We acknowledge that we
274 have based these measurements on brief exposures to cold, and that the profile of low-
275 temperature survival can be dependent on both the temperature and duration of exposure

276 (Sinclair et al. 2015); thus, experiments exploring longer cold exposures could reveal mortality at
277 higher temperatures. However, we note that many freeze-avoidant and chill-susceptible
278 arthropods can withstand long cold exposures (Bale 1993), and that we can reasonably expect
279 spiders from these Arctic and sub-Arctic habitats to be tolerant of long exposures to the
280 relatively mild sub-zero temperatures we explore here.

281 Spiderlings had much lower SCPs than other life stages. This could be because of their
282 small size and lack of feeding, both of which will favour low SCPs (Salt 1961; Zachariassen et
283 al. 2004), and may also be consistent with this life stage encountering sub-zero temperatures at
284 high altitude when dispersing by ballooning (Decae 1987; Foelix 2011). Unlike in other life
285 stages, we did observe some variation in SCP among *P. groenlandica* spiderlings which was
286 roughly consistent with expectations based on collection locality: high elevation-collected
287 individuals had lower SCPs than their low-elevation counterparts. In general, *Pardosa* spp. with
288 lower body mass tended to have lower SCP and CT_{max} . This suggests that future comparisons of
289 SCP and CT_{max} , among species should account for body size, especially since small animals tend
290 to have lower SCPs (Salt 1961; Zachariassen et al. 2004), and also more quickly dehydrate when
291 exposed to high temperatures, which may affect critical thermal limits and SCP (Harrison et al.
292 2012).

293 Arctic *Pardosa* reach sexual maturity in the early summer and die at the end of the
294 breeding season. It is the juveniles that overwinter, in some cases more than once (Buddle 2000).
295 For this reason, we expected greater low temperature tolerance in the juveniles compared to the
296 adults, but found no evidence of this, which implies that the juveniles likely significantly
297 increase their cold tolerance (and possibly even change cold tolerance strategy) in the lead up to

298 winter. We suggest that laboratory acclimation and seasonal comparisons will be necessary to
299 extrapolate this work to allow cold tolerance-based estimates of overwintering capacity.

300 The CT_{\max} of the Yukon and Greenland *Pardosa* were consistent with those reported for
301 other spiders: for example, +45.1 °C in *Misumenops asperatus* (Thomisidae) from New Jersey
302 (Schmalhofer 1999) and +46.9 °C in *Peucietia viridans* (Oxyopidae) from Tennessee (Hanna and
303 Cobb 2007). Surface temperatures in tundra can exceed 30 °C (SEA pers. obs. 6 July 2015 at
304 65.8°N in YT), so this high tolerance to high temperatures means that *Pardosa* will likely not
305 encounter temperatures close to their CT_{\max} and will therefore be able to take full advantage of
306 the summer growing season. We observed some variation in CT_{\max} among populations that is
307 consistent with the expectation that lower elevation (and latitude) populations of *P. hyperborea*
308 have higher CT_{\max} (and therefore presumably high-temperature tolerance) than their high
309 elevation counterparts.

310 Our data are useful for comparison with other studies reporting or comparing thermal
311 tolerances of arthropods measured during the growing season. However, the most significant
312 latitudinal differences in climate occur in winter (Williams et al. 2015). Like the Beringian
313 pseudoscorpion, also collected in Yukon (Anthony et al. 2016), the cold tolerance we measured
314 for these juvenile polar *Pardosa* would be insufficient to survive the temperatures we expect they
315 would encounter in the winter. In the absence of a capacity for substantial thermal buffering
316 (underlying permafrost will yield low soil temperatures), we expect that juveniles of these
317 species exhibit significant seasonal variation in cold tolerance and suggest that these seasonal
318 variations will be interesting to explore to understand the limits of thermal tolerance in polar
319 spiders.

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332

333 The datasets generated during and/or analysed during the current study are available from the
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335

336 **Compliance with Ethical Standards**

337 There are no conflicts of interest to declare.

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473

474 **Figure Captions**

475 **Fig. 1.** Critical thermal minima (CT_{\min}) of Yukon-collected *Pardosa* (adult female from the YT-
476 NWT border; white boxplots), of adult unsexed *P. glacialis* (YT-NWT border), and Greenland-
477 collected *P. groenlandica* (juvenile, low elevation). Boxes indicate quartiles and whiskers the
478 95th percentile, crosses indicate means; numbers indicate sample size.

479

480 **Fig. 2.** Relationship between (a) Critical thermal maximum (CT_{\max}) or (b) supercooling point
481 (SCP) and mass of *Pardosa* spiders from the Yukon Territory, Canada (solid symbols), and
482 Greenland (open circles). Species: *P.f.*=*P. furcifera*; *P.h.*=*P. hyperborea*; *P.g.*=*P. groenlandica*;
483 *P.l.*=*P. lapponica*; *P.m.*=*P. moesta*. Mean \pm standard error shown. We did not perform a formal
484 correlation because the number of species/populations is too small to satisfactorily account for
485 phylogeny.

486

487

488 **Tables**

489 **Table 1.** Collection details for *Pardosa* spiders in the Yukon Territory (Summer 2015), and
 490 Greenland (Summer 2016). F = adult females; M = adult males; J = juveniles; S = spiderlings,
 491 Low = low elevation; High = high elevation.
 492

Location name	Latitude, Longitude	Elevation (m)	Species, sexes, and life stages
<i>Yukon Territory</i>			
Tombstone Mtns	64.6°N, 138.3°W	1150	<i>P. lapponica</i> (F), <i>P. sodalis</i> (F)
Ogilvie Mtns	65.8°N, 137.8°W	837	<i>P. moesta</i> (F)
YT-NWT border	67.0°N, 136.2°W	647-1000	<i>P. lapponica</i> (F), <i>P. sodalis</i> (F), <i>P. moesta</i> (F), <i>P. glacialis</i> (adult, sex not recorded)
<i>Greenland</i>			
Narsarsuaq			
Low elevation	61.2°N, 45.4°W	s.l.-80	<i>P. furcifera</i> (J, F, M), <i>P. groenlandica</i> (S, J, F), <i>P. hyperborea</i> (J, F, M)
High elevation	61.1°N, 45.4°W	c. 450	<i>P. furcifera</i> (J, F, M), <i>P. groenlandica</i> (S, J, F, M), <i>P. hyperborea</i> (S, J, F)
Disko Island			
Low elevation	69.3°N, 53.5°W	50	<i>P. glacialis</i> (F)
Hot Springs	69.3°N, 53.5°W	50	<i>P. glacialis</i> (F)

493

494 **Table 2.** Survival of frozen and unfrozen Arctic *Pardosa* exposed to low temperatures. The
 495 Greenland low elevation spiders were from 0 to c. 80 m asl, and the high elevation were
 496 collected at c. 450 m. *Pardosa* were cooled until c. 50% froze and allowed to recover for 24 h at
 497 room temperature. Dead individuals were those that did not move or right themselves. CS – chill
 498 susceptible, FA – freeze-avoidant.
 499

	Frozen		Unfrozen		Strategy
	No. Alive	No. Dead	No. alive	No. Dead	
Greenland					
<i>Pardosa furcifera</i>					
Juvenile, low elevation	0	9	7	0	FA
Adult female, low elevation	0	5	5	0	FA
<i>Pardosa groenlandica</i>					
Juvenile, low elevation	0	5	5	0	FA
Juvenile, high elevation	0	8	6	0	FA
Adult female, low elevation	0	8	5	3	CS
Adult female, high elevation	0	6	2	1	CS
<i>Pardosa hyperborea</i>					
Juvenile, low elevation	0	10	6	0	FA
Adult female, low elevation	0	9	4	3	CS
Adult female, high elevation	0	8	5	2	CS
Yukon					
<i>Pardosa lapponica</i> , adult female	0	5	4	1	FA
<i>Pardosa moesta</i> , adult female	0	6	3	1	FA
<i>Pardosa sodalis</i> , adult female	0	5	4	1	FA

500

501

502

503 **Table 3.** Results of statistical comparisons of supercooling points and critical thermal maxima (CT_{max}) of Greenland- and Yukon-
504 collected *Pardosa* within species. Results are comparing within species among age groups (spiderling, juvenile, adult females) and
505 among collection locations separated by elevation (0-80 m asl, c. 450m asl). Results are from two-way ANOVA; df = degrees of
506 freedom. Asterisks indicate significant terms.
507

	Age			Elevation			Age × Elevation		
	<i>df</i>	<i>F</i> -ratio	<i>p</i> value	<i>df</i>	<i>F</i> -ratio	<i>p</i> value	<i>df</i>	<i>F</i> -ratio	<i>p</i> value
SCP									
<i>P. groenlandica</i> (omitting spiderlings)	2,59	139.6	<0.001*	1,59	2.8	0.101	2,59	6.5	0.003*
	1,45	24.1	<0.001*	1,45	1.1	0.307	1,45	2.0	0.165
<i>P. hyperborea</i> (omitting spiderlings)	2,56	228.0	<0.001*	1,56	0.4	0.509	-	-	-
	1,43	0.1	0.739	1,43	0.9	0.357	-	-	-
<i>P. furcifera</i>	1,45	4.3	0.043*	1,45	<0.1	0.969	1,45	0.5	0.468
CT_{max}									
<i>P. groenlandica</i>	1,30	0.02	0.898	1,30	2.2	0.150	-	-	-
<i>P. hyperborea</i>	1,38	11.9	0.001*	1,38	91.0	<0.001*	1,38	17.3	<0.001*
<i>P. furcifera</i>	1,22	22.0	<0.001*	1,22	2.5	0.128	-	-	-

508

509 **Table 4.** Supercooling points (SCP) of *Pardosa* spiders collected in Greenland and the Yukon
510 Territory (Canada). In Greenland, low elevation collections were below 80 m asl; high elevation
511 collections from c. 450 m asl. Yukon animals were from the YT-NWT border; see Table 1 for
512 further details on collection localities. There was no difference in SCP between female and male
513 *P. groenlandica* ($t_{6,0} = 0.312$, $p = 0.766$), *P. hyperborea* ($t_{13,4} = 1.210$, $p = 0.247$), or *P. furcifera*
514 ($t_{2,3} = 0.679$, $p = 0.558$); additional statistical comparisons are in Table 3.
515

Species and collection site	Spiderling	SCP: mean \pm sem, °C (n)		
		Juvenile	Adult Female	Adult male
Greenland				
<i>Pardosa furcifera</i>				
	Low elevation	-7.4 \pm 0.2 (12)	-7.0 \pm 0.2 (13)	-7.5 \pm 0.4 (3)
	High elevation	-7.6 \pm 0.3 (16)	-6.8 \pm 0.5 (8)	
<i>Pardosa groenlandica</i>				
	Low elevation	-19.7 \pm 1.0 (8)	-7.3 \pm 0.2 (15)	-6.3 \pm 0.2 (16)
	High elevation	-15.4 \pm 1.8 (8)	-7.9 \pm 0.4 (13)	-6.1 \pm 0.3 (5)
<i>Pardosa hyperborea</i>				
	Low elevation		-7.8 \pm 0.3 (10)	-7.8 \pm 0.2 (26)
	High elevation	-19 \pm 0.7 (14)	-8.2 \pm 0.6 (10)	-8.4 \pm 0.5 (11)
<i>Pardosa glacialis</i>				
	Low elevation		-7.6 \pm 0.1 (14)	
	Disko Island		-6.6 \pm 0.3 (14)	
Yukon				
	<i>Pardosa glacialis</i>		-6.8 \pm 0.3 (8)	
	<i>Pardosa lapponica</i>		-5.4 \pm 0.2 (10)	
	<i>Pardosa moesta</i>		-6.2 \pm 0.1 (10)	
	<i>Pardosa sodalis</i>		-5.9 \pm 0.2 (9)	

516

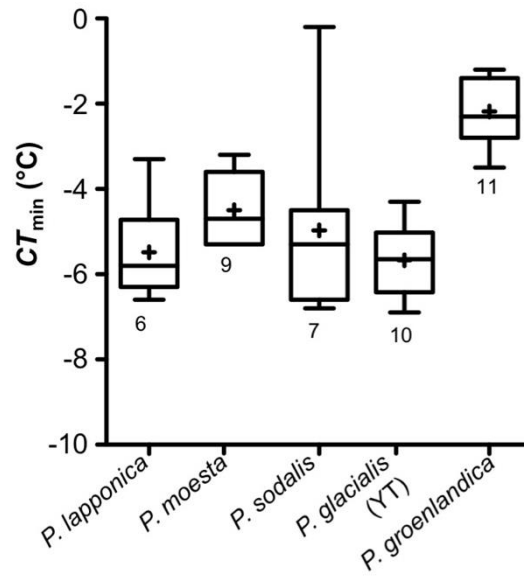
517

518 **Table 5.** Critical thermal maxima (CT_{max}) of *Pardosa* spiders collected in Greenland and the
 519 Yukon Territory (Canada). In Greenland, low elevation collections were below 80 m asl; high
 520 elevation collections from c. 450 m asl. See Table 1 for further details on collection localities.
 521 There was no difference in SCP between female and male *P. groenlandica* ($t_{6,0} = 0.312$, $p =$
 522 0.766), *P. hyperborea* ($t_{13,4} = 1.210$, $p = 0.247$), or *P. furcifera* ($t_{2,3} = 0.679$, $p = 0.558$); statistical
 523 comparisons are in Table 3.
 524

CT_{max} (mean±sem, °C (n))		
Species and collection site	Juvenile	Adult Female
Greenland		
<i>Pardosa furcifera</i>		
Low elevation	+43.4±0.4 (10)	+46.6 ±0.5 (11)
High elevation		+45.3±0.2 (4)
<i>Pardosa groenlandica</i>		
Low elevation	+45.1±0.2 (11)	+45.3±0.1 (10)
High elevation	+45.5±0.3 (12)	
<i>Pardosa hyperborea</i>		
Low elevation	+46.0±0.2 (11)	+43.6±0.2 (16)
High elevation	+42.3±0.3 (10)	+42.3±0.2 (5)
<i>Pardosa glacialis</i>		
Low elevation		+43.2±0.3 (14)
Disko Island (not sexed)		+45.9±0.3 (12)
Yukon		
<i>Pardosa glacialis</i>		
YT-NWT border		+46.6±0.4 (9)
<i>Pardosa lapponica</i>		
Tombstone Mtns		+42.9±3.1 (5)
YT-NWT border		+45.5±1.0 (6)
<i>Pardosa moesta</i>		
YT-NWT border		+44.7±0.5 (7)
<i>Pardosa sodalis</i>		
Tombstone Mtns		+46.4±0.5 (4)
YT-NWT border		+46.8±0.3 (3)

525
 526

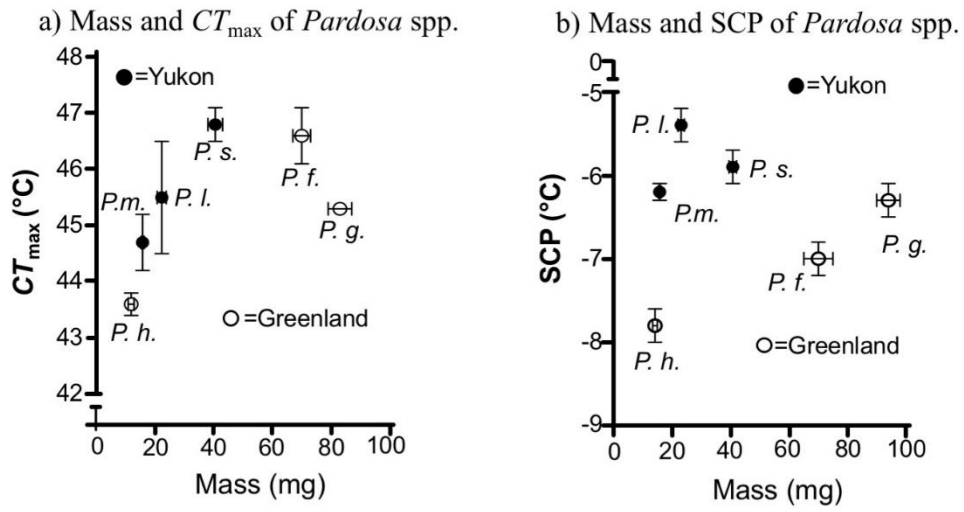
527



528

529 Figure 1

530



531

532

533 Figure 2

534