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1 **Variation in abundance and life history traits of two congeneric Arctic wolf**  
2 **spider species, *Pardosa hyperborea* and *Pardosa furcifera*, along local**  
3 **environmental gradients**

4

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15 **ABSTRACT**

16 The Arctic tundra is characterised by harsh conditions and environmental gradients are  
17 especially pronounced. Variation in functional traits along such gradients provide insights into  
18 the drivers of species abundance and distribution, and are particularly valuable in this region  
19 currently experiencing strong climate warming. Over three consecutive years, we analysed the  
20 interacting effect of two environmental factors, habitat and elevation, on the abundance, body  
21 size and clutch size in two common Low-Arctic invertebrate predators (Lycosidae, Araneae),  
22 *Pardosa furcifera* (Thorell 1875) and *Pardosa hyperborea* (Thorell 1872). Using generalised  
23 linear models, we firstly showed a habitat partitioning between *P. furcifera*, which dominated  
24 wet habitats like fens, and *P. hyperborea*, which was more associated with drier habitats like  
25 shrubs. Secondly, we found smaller body sizes at high elevation in *P. hyperborea*, a species  
26 that has a southern distribution in Greenland, and we identified season length as a major driver  
27 of the development in this species. In *P. furcifera*, a species likely more cold-adapted, we found  
28 no body size difference between elevations, suggesting that local conditions (e.g. prey  
29 availability or snowmelt timing) are more important in explaining body size variations. Finally,  
30 body size and clutch size were strongly correlated in both species, but clutch size was not  
31 affected by habitat or elevation. We argue that fecundity is likely influenced by trade-offs, and  
32 that considering additional complementary trait measurements would allow for a better  
33 understanding of the mechanisms underlying patterns in species life-history traits along  
34 environmental gradients.

35 Keywords: Converse Bergmann's rule, Latitudinal compensation, Southern Greenland, Trade-  
36 off, Body size, Fecundity

37 **DECLARATIONS**

38

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43 interest.

44 **Availability of data and material** (data transparency)

45 **Code availability** (software application or custom code)

46 **Authors' contributions:** All authors contributed to the study conception and design. The  
47 monitoring program at Narsarsuaq is led by TTH and carried out by numerous field assistants.  
48 All specimens were identified by CM. Data were generated, analysed, and interpreted by NV  
49 under the supervision of TTH and JP. The first draft of the manuscript was written by NV. All  
50 authors contributed to article revision and final approval.

## 51 INTRODUCTION

52           The Arctic tundra is characterised by harsh conditions like extreme cold temperatures  
53 and a brief growing season (Hobbie et al. 2021). Such conditions shape a diversity of habitat  
54 patches with pronounced local environmental gradients (e.g. in vegetation or in soil moisture;  
55 Hobbie et al. 2021; Hansen et al. 2016) across short distances. This in turn results in distinct  
56 spatial variation in arthropod community composition (Høye et al. 2018; Dahl et al. 2018; Hein  
57 et al. 2019a), a group that constitutes the majority of animal species in the region (Schmidt et  
58 al. 2017). Similarly, elevation also creates environmental variation and affects species  
59 distribution and development (Körner 2007; Hein et al. 2019b; Viel et al. 2022). At higher  
60 elevation, environments become more variable and less predictable, both in terms of abiotic  
61 (e.g. season length) and biotic (e.g. food availability) conditions (Blanckenhorn 1997;  
62 Hodkinson 2005). Elevational gradients are thus considered useful for studying variations in  
63 species abundance and life-history (Körner 2007; Høye et al. 2020). In this regard, Arctic  
64 ecosystems represent an opportunity to investigate underlying ecological processes through  
65 functional approaches, for instance via trait-based methods (*sensu* Violle et al. 2007), providing  
66 complementary insights to classic taxonomic studies (Bartomeus et al. 2016; Bonfanti et al.  
67 2018; Høye and Culler 2018; Wong et al. 2019).

68           Among functional traits, life-history traits represent a particularly valuable source of  
69 information because they are strongly linked to the fitness of organisms and are expected to be  
70 significantly sensitive to different environmental stressors (Moretti et al., 2017). Body size is  
71 certainly the most studied trait (e.g. Mammola et al. 2019; Koltz and Wright 2020; Monsimet  
72 et al. 2021) because it affects nearly all aspects of an organism (Kingsolver and Huey 2008)  
73 and reflects the conditions experienced during the development (Ameline et al. 2018). The well-  
74 known Bergmann's rule was developed to explain spatial variation in body size of individuals  
75 across latitudinal and altitudinal gradients (e.g. Ray 1960; McNab 1971; Meiri and Dayan

76 2003). It predicts that individuals would be larger at higher latitude or altitude because a smaller  
77 surface-area-to-volume ratio reduces heat loss. On the other hand, the Converse Bergmann's  
78 rule (see e.g. Blanckenhorn and Demont 2004) states that the active season length is more  
79 important than temperature in some cases (e.g. Blanckenhorn 1997; Høye et al. 2009). It  
80 predicts smaller body sizes with increasing elevation as a decreasing season length limits the  
81 amount of time for foraging, growth and maturation. Lastly, body size is interesting because it  
82 is highly correlated to other life-history traits like fecundity, especially in invertebrates (e.g.  
83 Dearn 1977; Kingsolver 1983; Puzin et al. 2011; Berry et al. 2018). This trait thus represents a  
84 good metric to understand variation in e.g. maternal investment or reproductive output along  
85 environmental gradients (Ameline et al. 2018; Wolz et al. 2020).

86         Among terrestrial arthropods, which are known to quickly respond to environmental  
87 changes (Spiller et al. 2017; Beckers et al. 2018; Høye 2020), wolf spiders are often regarded  
88 as relevant bio-indicators because of their importance in ecological communities as prey and  
89 predators (Marshall and Rypstra 1999; Jocqué and Alderweireldt 2005; Foelix 2011). They  
90 usually exhibit high spatial variation in abundance, reflecting their physiological tolerance to  
91 different environmental conditions, like humidity, temperature, or salinity for instance (see e.g.  
92 DeVito et al. 2004; Frick et al. 2007; Pétilion et al. 2011). In Arctic ecosystems, wolf spiders  
93 are dominant top-predators in the food web (Høye and Hammel 2010; Schmidt et al. 2017) and  
94 are present at high densities in many habitats (Bowden and Buddle 2012; Høye et al. 2021).  
95 Finally, females lay their eggs into cocoons that they transport by keeping them attached to  
96 their spinnerets until they hatch (Jocqué and Alderweireldt 2005; Piacentini and Ramírez 2019),  
97 making it possible to obtain concomitant specimen-specific trait measurements of individuals  
98 and their progeny. Therefore, wolf spiders such as *Pardosa* species, offer the possibility of  
99 studying co-variations between such traits, and sometimes even of investigating potential trade-  
100 offs in maternal investment (e.g. Hendrickx and Maelfait 2003; Ameline et al. 2017).

101           Whilst global warming is particularly strong in the Arctic (IPCC 2019), transform tundra  
102 landscapes (e.g. Frost et al. 2013; Rich et al. 2013; Hobbie et al. 2017; Bowden et al. 2018),  
103 and is becoming a concerning threat to arthropods (Høye 2020; see also Halsch et al. 2021), a  
104 need for more insights about the Arctic biodiversity from a wide range of locations is needed  
105 (Høye et al. 2020; Taylor et al. 2020). In this study, based on three consecutive years of  
106 sampling, we investigate habitat selection of two common Arctic wolf spider species, *Pardosa*  
107 *hyperborea* (Thorell 1872) and *Pardosa furcifera* (Thorell 1875), and we analyse the interacting  
108 effects of habitat and elevation on two life-history traits, i.e. body size and clutch size. In other  
109 words, we try to identify the role of two major factors that act at two different scales, on the  
110 two most abundant predators species of the study area (Høye et al. 2018), and thus a key  
111 component of the trophic web in the region. At this latitude, the relative importance of local-  
112 (e.g. micro-habitat factor effects in Hansen et al. 2016) vs broad-scale factors (Hein et al. 2019)  
113 in driving arthropod populations has not been clearly understood. Moreover, the way elevation  
114 affects ectotherms is still debated (e.g. Blanckenhorn and Demont 2004). We thus aim to better  
115 understand how two locally dominant species are spatially distributed, and to determine the  
116 importance of environmental factors for these species by analysing functional trait variation.  
117 We predict that the distribution of the studied species over space is determined by both  
118 environmental factors, with abundances decreasing with increasing elevation, and a habitat  
119 partitioning with more individuals of *P. hyperborea* in relatively dry and shrubby habitats, e.g.  
120 shrub, and more individuals of *P. furcifera* in relatively wet and open habitats, e.g. fens  
121 (Marusik 2015; Hansen et al. 2016). Further, we predict that the number of eggs per cocoon (or  
122 clutch size), as proxy for individual fecundity, is determined by maternal body size (Marshall  
123 and Gittleman 1994), i.e. that these traits are positively correlated. Finally, we predict a  
124 predominant effect of the broad-scale factor on measured traits, i.e. elevation, compared to the  
125 local factor, i.e. habitat, in both species (Hein et al. 2019b), and more specifically, a Converse

126 Bergmann's Rule pattern (Blanckenhorn and Demont 2004), i.e. individuals with smaller body  
127 sizes and smaller clutch sizes at higher elevation sites compared to lower elevation sites.

128

## 129 **MATERIALS AND METHODS**

### 130 *Studied species*

131         Whilst *Pardosa* species from temperate latitudes are known to have annual life-cycles,  
132 in northern zones, it has been reported that boreal and Arctic wolf spider species usually show  
133 a biennial life-cycle model (e.g. Høye et al. 2009). Young are developing as juveniles and sub-  
134 adults two winters in a row, and mature as adults the third active season where they breed and  
135 die (Buddle 2000; Pickavance 2001; Ameline et al. 2017; Viel et al. 2022).

136 Here, the studied *Pardosa* models represent the two most abundant spider species of the region  
137 (Høye et al. 2018), occurring in the same geographic area and sharing similar broad  
138 environmental conditions, i.e. being sympatric. *Pardosa hyperborea* on the one hand, a fairly  
139 well studied species (e.g. Pickavance 2001; Viel et al. 2022) measuring between 4.5 and 5.6  
140 mm in body length (Paquin and Dupérré 2003), is widespread over boreal and Low-Arctic areas.  
141 It usually occurs in open forests and amongst lichens in the tundra (Dondale and Redner 1990;  
142 Paquin and Dupérré 2003; Marusik 2015; Nentwig et al. 2021). In Arctic landscapes  
143 specifically, the species is described as indicative of heath and shrub habitats (Hansen et al.  
144 2016; Høye et al. 2018). On the other hand, *P. furcifera*, a bigger spider measuring between 7.2  
145 and 8.7 mm in body length, seems to be a more northerly species known from Low-Arctic and  
146 alpine environments (Dondale and Redner 1990; Paquin and Dupérré 2003; Marusik 2015).  
147 The species is usually found in a variety of habitats (Hansen et al. 2016; Høye et al. 2018) but  
148 is predominantly found on moss layers and in snow beds, seemingly preferring moist areas  
149 (Dondale and Redner 1990; Marusik 2015).

150

151 *Study area and experimental design*

152           The study area is located near Narsarsuaq, South Greenland (61.16°N, 45.40°W; *Fig.*  
153 *1*), in the Sub-Arctic/Low-Arctic transition zone where the vegetation cover is continuous and  
154 where shrubs are frequent (Polunin 1960; CAFF 2013). The experimental design (see Høye et  
155 al. 2018 for more details) consisted of transects of yellow pitfall traps each 10 cm in diameter,  
156 containing a 50% propylene glycol:water mixture as preservative with a few drops of detergent  
157 to break the surface tension of the trapping liquid.

158           Transects have been installed in the two most common habitats of the study area,  
159 constituting a mosaic across the landscape, i.e. either in fen type habitats, consisting in 2 rows  
160 of 40 m long with 9 pitfall traps 5 m apart, or in tall shrub type habitats, consisting in 2 rows of  
161 20 m long with 5 pitfall traps 5 m apart. The limited size of shrub patches in studied sites did  
162 not allow to make the transects as long as the fen transects (Høye et al. 2018). The fen type  
163 patches were overall characterised by wet soils and by a relatively short vegetation composed  
164 of mosses, *Betula glandulosa* and different species of *Carex*, with higher dominance of lichens  
165 at higher elevations (Høye et al. 2018). The shrub type patches were overall distinguished by  
166 drier soils and by a relatively high cover of dwarf shrubs like *Vaccinium uliginosum* and  
167 *Empetrum hermaphroditum* and lichens, whilst some parts were almost completely covered by  
168 *Salix glauca* with occasional herb species like *Campanula rotundifolia* (Høye et al. 2018).

169           The experimental set-up was designed to capture fine-scale environmental gradients, as  
170 for instance, some traps were installed in drier parts of fen patches and in shorter vegetation  
171 surrounding shrub patches, i.e. in more moor-heath type habitats. However, here we are looking  
172 at the habitat scale since wolf spiders are known to be active wandering hunters having large  
173 movement ranges (Morse 1997; Kiss and Samu 2000; but see also Ahrens and Kraus 2006).

174           In total, in each habitat type, three transects have been set up at 50 m above sea level,  
175 i.e. at low elevation, and two transects have been set up at 450 m above the sea level, i.e. at high

176 elevation, which represents a total of 140 pitfalls traps. Monthly average ground surface  
177 temperatures at low sites are typically 1-2°C degrees warmer during summer than at high sites  
178 (data for the months of June, July and August, from the years 2016 and 2017, unpubl. data). In  
179 this study, samples from only one transect line in each plot have been used, i.e. across 70 pitfall  
180 traps, while samples from the other transect have been kept for future molecular analyses. Traps  
181 were collected weekly during the growing seasons of the period 2015–2017.

182

### 183 *Laboratory work*

184 In the laboratory, spiders were identified to species level and samples containing female wolf  
185 spiders were kept separate with their cocoon if any. Over the four wolf spider species that were  
186 collected, i.e. *P. furcifera*, *P. hyperborea*, *Pardosa groenlandica* (Thorell 1872) and *Arctosa*  
187 *insignita* (Thorell 1872), the last two were omitted due to low sample size (17 and 76 females  
188 of *P. groenlandica* and *A. insignita*, respectively. Only one individual of *P. groenlandica* and  
189 *A. insignita* with a cocoon were found over the three years. Females of the two selected species  
190 having a cocoon were then photographed individually on laminated graph paper using a stereo  
191 microscope and a smartphone camera. The carapace width (i.e. prosoma width) was measured  
192 from the pictures by calibrating size against the graph paper using the software ImageJ  
193 v.1.8.0\_112. As the prosoma is known to be fixed in adult spiders, i.e. not varying with diet or  
194 hydration for example, this part is usually used as a proxy for the body size of individuals (e.g.  
195 Hagstrum 1971; Jakob et al. 1996; Pickavance 2001; Legault and Weis 2013). Finally, the  
196 cocoons were opened and their content counted. Specimens are preserved in 75% ethanol and  
197 stored at the Natural History Museum Aarhus, Denmark.

198

### 199 *Statistics*

200 Data from all three years were combined in the analyses to focus on general spatial  
201 trends, and we only considered female individuals. Spiders are indeed known to show  
202 differences in response to environmental drivers between sexes (e.g. Pekár and Vaňhara 2006;  
203 Høye and Hammel 2010; Bowden et al. 2013), and we are not investigating sexual size  
204 dimorphism here.

205 To investigate the abundance of each species across elevations and habitats, we built a  
206 Generalized Linear Model (GLM) with a Poisson distribution for *P. furcifera* and a GLM using  
207 a negative binomial distribution for *P. hyperborea* to overcome overdispersion of residuals  
208 (package “MASS”: Venables and Ripley 2002). We then analysed the effect of both elevation  
209 and habitat type on the carapace width of specimens by running a simple linear regression  
210 model for the two studied species. The relationship between body size and clutch size was tested  
211 for each species using GLMs with a negative binomial distribution, and predictions from these  
212 models were visualized with the package “ggplot2” (Wickham 2016). Finally, we tested the  
213 effect of elevation and habitat on clutch size for each species by building GLMs with a negative  
214 binomial distribution, including female body size as predictor. Analyses of the relation between  
215 body size and clutch size were made on clearly identified mother/cocoon pairs. However, both  
216 *P. hyperborea* and *P. furcifera* females have been shown to be able to produce two clutches in  
217 one active season with the second clutch being smaller than the first (Viel et al. 2022).  
218 Therefore, in order to avoid potentially mixing smaller second clutches with the larger first  
219 clutches, we used the method in Viel et al. (2022) to only keep clutches from the first laying  
220 episode. Specifically, we found no evidence of differences in date thresholds amongst species  
221 and elevations and thus excluded clutches collected after week 31 of the year (i.e. around  
222 August 1<sup>st</sup>; see details in Online Resource 1).

223 For each model, the linearity and the normality (when required) of residuals was  
224 checked from plots of residuals versus predicted values and QQ-plots with a Shapiro-Wilk test

225 (package “RVAideMemoire”: Hervé 2019). Significances of explanatory variables and factors  
226 were tested with ANOVA tests type II (package “car”: Fox and Weisberg 2019). The compared  
227 means, presented with standard errors, were estimated marginal means obtained with the  
228 package “emmeans” (Lenth 2019). All analyses were performed using the software R v.3.6.2  
229 (R Core Team 2019).

230

## 231 **RESULTS**

### 232 *Abundances*

233 Over the three years, habitat had a significant effect on the abundance of *P. furcifera* (Table 1),  
234 with more female individuals per pitfall trap along transects in fens than in shrub habitats ( $1.79$   
235  $\pm 0.09$ ,  $n = 946$  vs.  $1.53 \pm 0.06$ ,  $n = 314$ ; Log-likelihood ratio test:  $\chi^2 = 5.67$ ,  $df = 1$ ,  $p = 0.0172$ ;  
236 Fig. 2a). Elevation did not show any significant effect on the abundance of this species. For *P.*  
237 *hyperborea*, we found a significant interaction between habitat and elevation on the abundance  
238 of females (Log-likelihood ratio test:  $\chi^2 = 4.10$ ,  $df = 1$ ,  $p = 0.0428$ ; Table 1). Specifically, in  
239 both habitat types there were significantly more females individuals per pitfall trap along  
240 transects at low elevation than at high elevation (*in shrubs*:  $4.46 \pm 0.17$ ,  $n = 2259$  vs.  $2.59 \pm$   
241  $0.18$ ,  $n = 471$ ; *in fens*:  $2.85 \pm 0.10$ ,  $n = 1951$  vs.  $2.08 \pm 0.15$ ,  $n = 416$ ) and more female specimens  
242 per pitfall trap along transects in shrubs than in fens at low elevation ( $4.46 \pm 0.17$ ,  $n = 2259$  vs.  
243  $2.85 \pm 0.10$ ,  $n = 1951$ ; Fig. 2b). Finally, the model showed that the difference in abundance  
244 between habitats at high elevation was not significant for this species.

245

### 246 *Body size and fecundity*

247 We found a significant and positive effect of carapace width on the number of eggs per cocoon  
248 for *P. furcifera* (Log-likelihood ratio test:  $\chi^2 = 17.15$ ,  $df = 1$ ,  $p < 0.0001$ ), as well as for *P.*  
249 *hyperborea* (Log-likelihood ratio test:  $\chi^2 = 89.33$ ,  $df = 1$ ,  $p < 0.0001$ ; Table 1; Fig. 3).

250 Concerning the effect of environmental factors on body size, for *P. furcifera* the linear model  
251 showed no significant effect of elevation on the carapace width of females ( $3.01 \pm 0.04$  mm,  $n$   
252 = 75 at low elevation vs.  $2.99 \pm 0.03$  mm,  $n = 27$  at high elevation; Sum of squares = 0.01;  $F_{1,99}$   
253 = 0.16;  $p = 0.0287$ ; Table 1). However, females were significantly larger in fen than in shrub  
254 habitats ( $3.05 \pm 0.03$  mm,  $n = 70$  vs.  $2.95 \pm 0.04$  mm,  $n = 32$ ; Sum of squares = 0.22;  $F_{1,99} =$   
255 4.92;  $p = 0.6935$ ; Table 1; Fig. 4a). By contrast, for *P. hyperborea*, analyses revealed no  
256 significant effect of habitat on the carapace width of females ( $1.75 \pm 0.01$  mm,  $n = 182$  in fens  
257 vs.  $1.75 \pm 0.01$  mm,  $n = 132$  in shrubs; Sum of squares = 0.001;  $F_{1,311} = 0.08$ ;  $p = 0.7779$ ; Table  
258 1), but there were significantly larger individuals at low elevation than at high elevation ( $1.79$   
259  $\pm 0.01$  mm,  $n = 267$  vs.  $1.71 \pm 0.02$  mm,  $n = 47$ ; Sum of squares = 0.20;  $F_{1,311} = 10.58$ ;  $p =$   
260 0.0013; Table 1; Fig. 4b). Finally, our models testing the influence of the studied factors on  
261 clutch sizes did not show any significant effect of habitat or elevation for either *P. furcifera*  
262 ( $85.37 \pm 3.31$ ,  $n = 70$  in fens vs.  $84.80 \pm 4.20$ ,  $n = 32$  in shrubs; and  $80.01 \pm 2.86$ ,  $n = 75$  at low  
263 elevation vs.  $90.49 \pm 4.77$ ,  $n = 27$  at high elevation) or *P. hyperborea* ( $21.65 \pm 0.61$ ,  $n = 182$  in  
264 fens vs.  $22.51 \pm 0.69$ ,  $n = 132$  in shrubs; and  $22.73 \pm 0.42$ ,  $n = 267$  at low elevation vs.  $21.44 \pm$   
265  $0.96$ ,  $n = 47$  at high elevation; Table 1; Online Resource 1). However, for *P. furcifera*, we found  
266 a tendency towards larger clutch sizes, i.e. more eggs per cocoon, at higher elevations, but this  
267 trend was only marginally significant (Log-likelihood ratio test:  $\chi^2 = 3.68$ ,  $df = 1$ ,  $p = 0.0551$ ).

268

## 269 **DISCUSSION**

### 270 *Combined effects of habitat and elevation on abundance*

271 The abundance of female wolf spiders varied amongst habitat types and elevation in  
272 different ways between the two studied species. Whilst *P. furcifera* was more common in fen  
273 habitats and showed similar abundances between elevations, *P. hyperborea* was fluctuating

274 between elevations according to habitats, being more common at low elevation and almost  
275 twice as abundant in low elevation shrub patches compared to low elevation fen patches.  
276 These results, based on a consistent dataset, indicate that *P. furcifera* is more related to wet  
277 habitats than *P. hyperborea*, which is in line with earlier anecdotal evidence (Dondale and  
278 Redner 1990; Marusik 2015). We also provide a better understanding of the ecology of a species  
279 that is rather poorly documented. In the Arctic, wetlands are known to support high prey  
280 availability for predators like spiders (Böcher et al. 2015; Bowden et al. 2015; Loboda et al.  
281 2018; Koltz et al. 2018), which select their prey mostly according to abundance (Wirta et al.  
282 2015). Local conditions like habitat characteristics thus appear to be more important for the  
283 distribution of this species than larger scale factors, e.g. temperature gradients induced by  
284 changes in elevation. This idea is supported by the fact that abundances did not differ  
285 significantly between elevations, which therefore contradicts our first hypothesis of a negative  
286 effect of elevation on population abundance.

287         For *P. hyperborea*, our first hypothesis was only partly confirmed. Individuals were  
288 indeed more common at low elevation in both habitat types, but we observed a partitioning  
289 between habitats only at lower elevations. Our results suggest that at low elevations, females of  
290 *P. hyperborea* are more abundant in habitats that tend to be drier, like shrub patches, contrasting  
291 with its congeneric *P. furcifera*. This is in accordance with previous findings describing *P.*  
292 *hyperborea* as indicative of heath-like and shrub-like landscapes (Marusik 2015; Hansen et al.  
293 2016; Høye et al. 2018).

294         With increasing altitude, growth conditions deteriorate (Blanckenhorn 1997; Hodkinson  
295 2005; Körner 2007) as abiotic conditions become more severe and resources generally become  
296 scarcer (Bowden et al. 2013; Ameline et al. 2018). One can thus expect lower populations sizes  
297 at high elevation compared to low elevation in line with patterns of species richness (Bowden  
298 and Buddle 2010). Hence, *P. hyperborea* would only show habitat preferences at low elevation

299 with similar abundances at higher altitudes, because conditions at high elevation might be  
300 especially restrictive for this species and would reduce the advantages of preferred habitats. In  
301 other words, the distribution of *P. hyperborea* in Arctic ecosystems would be determined by  
302 local conditions in favourable contexts, e.g. at low elevations, but by broader drivers like  
303 climatic gradients in harsher conditions, e.g. at higher elevations. Similarly, conditions at high  
304 elevation in the study area could be close to the ones at the northern edges of the climatic range  
305 boundaries of *P. hyperborea*, which would explain the significant spatial variation in habitat  
306 specificity between elevation (Oliver et al. 2009). In this case, such pattern is likely to change  
307 over time because of the quick warming occurring in the Arctic region, e.g. high elevation sites  
308 could become suitable enough for the species to observe clear habitat preferences in  
309 populations. In comparison, *P. fuscifera* would be more adapted to cold environments than its  
310 congeneric. This species is known from more northern latitudes (Dondale and Redner 1990;  
311 Marusik 2015; see also Hansen et al. 2016; Ameline et al. 2017) which could explain why  
312 densities are not affected by elevation in this species, especially in an area far from its northern  
313 range limit.

314         Despite our robust methodology, it is likely that we were not able to sample the entire  
315 active season. Indeed, local weather data suggest that temperatures generally remain positive at  
316 the study site for the period of the season corresponding to 3-4 weeks after our last trapping  
317 (i.e. an average of 5-10 °C between weeks 37 to 39, for the period 2012-2016; Høye, unpubl.  
318 data). As phenology of arthropods like spiders varies across elevations (e.g. Viel et al. 2022),  
319 an incomplete sampling season could have introduced a bias towards high elevation sites where  
320 the season is shorter, and thus where the information about abundances may have been better  
321 captured over time compared to low elevation sites. However, considering the relatively high  
322 number of traps we used for the study and because we are looking for patterns across a three

323 years period, we assume that our results would have remained the same even with a longer  
324 season.

325

### 326 *Body size*

327 We found that elevation did not have any effect on the body size of *P. furcifera*, but that  
328 the habitat did, with larger females in fen than in shrub patches. Our third hypothesis, which  
329 predicted that elevation is an important driver of body size variation with individuals following  
330 the Converse Bergmann's Rule, is therefore not supported for *P. furcifera*. On the contrary,  
331 females of *P. hyperborea* were smaller at high elevation with no significant effect of habitat,  
332 which confirms our third hypothesis for this species. The pattern of body size thus appears to  
333 be species-specific (see also Ameline et al. 2018), and the lack of an elevational effect in *P.*  
334 *furcifera* supports the idea that this species is cold-adapted and less sensitive to variation in  
335 growing season temperatures than *P. hyperborea*.

336 Our results for *P. furcifera* are in agreement with previous studies investigating different  
337 wandering spider species, whose conclusions show that elevation is not always a factor  
338 explaining the body size of individuals (e.g. *A. insignita* in Greenland: Høye and Hammel 2010;  
339 *Myro kerguelenensis* in a Sub-Antarctic island: Lee et al. 2012; *Alopecosa aculeata* in Canada:  
340 Bowden et al. 2013). Several non-exclusive arguments can explain this observation. Firstly, the  
341 lack of an elevational pattern was explained in *Pardosa palustris* in Southern Norway (Beckers  
342 et al. 2020) by short and long-distance dispersal of individuals during all life stages (e.g.  
343 ballooning of spiderlings, see Foelix 2011). However, we argue that it is more likely that the  
344 elevational difference between our sampling stations, i.e. 400 meters, is not large enough to  
345 generate an effect on the body size of *P. furcifera*. Such explanation is supported by the findings  
346 of Ameline et al. (2018) on *Pardosa glacialis* in Zackenberg (Greenland). Therefore, it would  
347 be relevant to extend the elevational gradient or to set up the experiment at higher latitudes to

348 compare more extreme conditions, especially for *P. furcifera*. On the other hand, it could be  
349 that organisms living at high latitudes or altitudes are able to compensate for seasonal time  
350 constraints by growing faster compared to their low latitude or altitude conspecifics  
351 (Blanckenhorn and Demont 2004). This phenomenon is referred to as the “countergradient  
352 variation”, or “latitudinal compensation”, and would be equivalent to the Converse Bergmann’s  
353 rule but from a perspective of a genetic response of individuals (Blanckenhorn and Demont  
354 2004). According to this hypothesis, individuals of *P. furcifera* at high elevations would  
355 compensate for the effect of a shorter season length by growing faster and reach similar body  
356 sizes as populations at lower elevation.

357         The altitudinal pattern in *P. hyperborea* seems easier to explain, as it matches with the  
358 Converse Bergmann’s rule. A decreasing body size concomitant with an increase in elevation  
359 would be the consequence of a shorter season length, leading to a shorter time available for  
360 growth and development (Blanckenhorn and Demont 2004). Such a pattern has been  
361 documented in four *Pardosa* species in Norway by Otto and Svensson (1982), where females  
362 were declining in size with elevation. The same relation between elevation and body size was  
363 documented in *P. glacialis* and *P. groenlandica* on Disko Island, Greenland by Høye and  
364 Hammel (2010). The authors argued that a contracting season length along elevational gradients  
365 would induce smaller growth increments during moults or fewer moults in individuals. Such  
366 variation in the number of instars required to reach maturity is a common feature in spiders  
367 (Deevey 1949; Edgar 1972; Buddle 2000). Additionally, a trend of decreasing size could be  
368 related to resource limitation at higher elevation, as already discussed above. More precisely,  
369 Chown and Gaston (1999) showed that ectotherms having a generation time that constitutes a  
370 significant proportion of the growing season are substantially influenced by the season length,  
371 because of constraints on resource availability (see also Chown and Klok 2003; Horne et al.  
372 2015). *Pardosa* species studied from high altitudes and northern latitudes usually require more

373 than one year to complete their development, spending sometimes two active seasons as  
374 juvenils and sub-adults (Schmoller 1970; Buddle 2000; Frick et al. 2007; Høye et al. 2009).  
375 Therefore, the pattern we describe in *P. hyperborea* is probably ascribed to a seasonality effect  
376 of resource availability, as found in *P. palustris* (Hein et al. 2019). Elevation is therefore likely  
377 more important for spatial variation in body size variation in this species than local factors such  
378 as habitat characteristics..

379 Females of *P. furcifera* were both more abundant and bigger in wet habitats. Food  
380 quality and quantity are thought to be important drivers of body size in terrestrial arthropods,  
381 including wolf spiders (Miyashita 1968; Bowden et al. 2015; Hein et al. 2019b). Although  
382 Arctic spiders are described as generalist species (Wirta et al. 2015), it could also be that food  
383 resources from wetlands better fit the nutritional needs of *P. furcifera* (Greenstone 1984; García  
384 et al. 2018; but see Eitzinger et al. 2019). An alternative interpretation could be that the present  
385 pattern is linked to snow dynamic, an abiotic parameter that influences Arctic arthropods in  
386 many ways (e.g. Legault and Weis 2013; Hein et al. 2014; Beckers et al. 2018). Bowden et al.  
387 (2015) for instance, proposed that later snowmelt in wetter patches would lead to a delayed  
388 maturation for overwintering sub-adults. Knowing that a longer development time has a  
389 positive effect on the body size of individuals (Roff 1980; Høye and Hammel 2010; Ameline  
390 et al. 2018) and that local topography controls the snow-cover dynamic (Wundram et al. 2010),  
391 a late snowmelt in wet habitats could explain the bigger individuals observed in *P. furcifera*.

392

### 393 *Fecundity*

394 We found a strong positive influence of maternal body size on clutch size in both  
395 species. Moreover, in both species the fecundity did not differ between habitat types and  
396 elevation. A positive relationship between body size and clutch size is common in wolf spiders  
397 as well in other spider families (e.g. Wise 1975; Simpson 1993; Marshall and Gittleman 1994;

398 Ameline et al. 2018), and has been reported across a diversity of habitat types (e.g. Eberhard  
399 1979; Killebrew and Ford 1985; Simpson 1995; Hein et al. 2018). This relationship explains  
400 the difference in reproductive output with *P. furcifera* producing bigger clutches than *P.*  
401 *hyperborea*. According to the metabolic theory of ecology (Brown et al. 2004), larger females  
402 can retain more energy for reproduction. Thereby, larger individuals can increase their  
403 fecundity more efficiently than smaller individuals, and ultimately their fitness (Ameline et al.  
404 2018).

405         It is commonly observed that resource limitations lead to lower fecundity in organisms  
406 (Ameline et al. 2017), with increasing elevation bringing harsher abiotic conditions (e.g. Körner  
407 2007). However, the effect of elevation on wolf spider fecundity appears to be inconsistent over  
408 space and between species. For instance, Ameline et al. (2018) investigated this topic for several  
409 lycosid species in several locations. Similarly to our finding (50-450m elevation gradient), the  
410 authors did not find an effect of elevation on the clutch size of *P. hyperborea* in Godthaabsfjord  
411 (ca. 0-700m elevation gradient) and Narsarsuaq (ca. 50-450m elevation gradient) in Greenland.  
412 But they also report a negative effect of elevation on fecundity for the same species at  
413 Kobbefjord (0-200m elevation gradient) in Greenland. In *P. palustris* in Iceland (ca. 0-400m  
414 elevation gradient) and Faroe Islands (samples collected at 350m), and in *P. glacialis* in  
415 Zackenberg (0-200m elevation gradient) in Greenland, the researchers did not observe any  
416 altitude-fecundity relationship either. On the contrary, Bowden et al. (2013) found that females  
417 of *Pardosa lapponica* in the Low-Arctic Canada (ca. 650-1450m elevation gradient) produced  
418 fewer progeny at higher elevations and that in *Pardosa uintana*, females collected at the highest  
419 spots were the ones showing the lowest fecundity as well. Finally, Punzo and Farmer (2006)  
420 reported smaller clutches from high elevation study sites in females of *Pardosa sierra* (ca. 900-  
421 1800m elevation gradient). Therefore, clutch size is not always following the same pattern  
422 across space and species, and although body size of females is strongly related to this

423 reproductive trait, it is likely not the only driving parameter of fecundity (Buddle 2000).  
424 Hodkinson (2005) for instance, summarised several examples of insects species that show  
425 declining fecundity with increasing elevation, and relates these observations to a potentially  
426 lower food quality at high elevation sites (see also Deevey 1949). He also proposed that local  
427 topography causes important microclimatic variations, which would determine the reproductive  
428 success of insects by producing effects over short vertical distances overriding broader  
429 elevational trends (but see Hein et al. 2019b).

430 In *P. furcifera*, clutch size was not significantly affected by elevation either, although,  
431 we found a tendency towards a higher number of eggs per clutch at high elevation. We argue  
432 that the high mobility of wolf spiders (Morse 1997; Beckers et al. 2020) combined with  
433 behavioural traits such as sun basking (Hodkinson 2018) would allow individuals to buffer the  
434 impact of harsh conditions. This would result in a reduced elevational cline for fecundity, e.g.  
435 in *P. hyperborea*, or even in a positive effect of elevation in cold-adapted species like *P.*  
436 *furcifera*. Alternatively, it has been suggested that larger amounts of snow at higher elevations  
437 (Hodkinson 2005) creates a more stable and warmer subnivean thermal environment that may  
438 reduce the high metabolic costs of overwintering (Legault and Weis 2013). According to this  
439 idea, *P. furcifera* might perform better than its congeneric under colder conditions, females at  
440 high elevation would use less energy to survive during the inactive season and would be able  
441 to invest more energy into reproduction during the active season than females at lower  
442 elevation. Similarly, Beckers et al. (2020) suggested that environmental conditions at high  
443 elevation could be less detrimental for ground-dwelling arthropods than what is usually  
444 assumed, because of a lower and a less dense vegetation cover that would lead to a higher solar  
445 irradiance. In such context where temperatures can rise very quickly, arthropods could rapidly  
446 respond by showing a higher activity that may result in higher reproductive rates (Hein et al.  
447 2018).

448

## 449 CONCLUSION

450 In this study, we analysed the interacting effect of elevation and habitat along local  
451 environmental gradients on the spatial distribution and two reproductive traits in *P. furcifera*  
452 and *P. hyperborea*. These two wolf spider species co-occurring in the same habitats and thus  
453 sharing similar environmental conditions, are very abundant in the Low-Arctic (Marusik and  
454 Koponen 2002; Bowden and Buddle 2012) and are considered as top predators in the trophic  
455 web (Schmidt et al. 2017). In spite of being closely related, we showed that the two species are  
456 responding in different ways to environmental factors, in terms of abundance but also  
457 morphologically. Specifically, we identified a spatial partitioning with *P. furcifera* being more  
458 common in wetter habitats and *P. hyperborea* being more abundant in shrub-dominated  
459 habitats. The distribution of these species across the tundra are thus driven by local  
460 environmental conditions like habitat characteristics. Moreover, we showed contrasting effects  
461 of abiotic factors on the body size of females. The body size of *P. hyperborea* was determined  
462 by elevation, displaying a pattern corresponding to the Converse Bergmann Rule, i.e. smaller  
463 individuals at high elevation. In contrast, the body size of *P. furcifera* was not influenced by  
464 elevation, likely because this species is adapted to colder conditions. Body size variation in this  
465 species was driven by habitat characteristics, with bigger individuals found in fen patches with  
466 likely higher availability of prey and later snowmelt timing. Finally, we showed that clutch size  
467 was strongly and positively related to the body size of females in both species, but that fecundity  
468 is likely also influenced by other parameters, e.g. inherent metabolic efficiency of species under  
469 cold conditions, or abiotic factors like temperature, solar irradiance or snow amount. Indeed,  
470 we did not observe any effect of habitat or elevation on such life-history trait. Body size and  
471 clutch size are therefore probably influenced by several factors whose effect might be additive  
472 or synergistic but that are difficult to detect and unravel. To better understand resource

473 allocation for reproduction in spiders like *Pardosa* species allocate for reproduction (see  
474 Marshall and Gittleman 1994; Fox and Czesak 2000), fecundity could also be assessed by  
475 measuring other metrics such as the size of eggs, a well-studied life-history trait (e.g. Pétilon  
476 et al. 2009; Berry et al. 2018) which would be relevant to consider for further trait-based studies.

477 To conclude, we argue that wolf spiders hold a great bio-indicator potential in northern  
478 latitudes, particularly relevant in a context of rapid climatic changes that will probably affect  
479 the entire Arctic trophic web (Hodkinson 2005; Schmidt et al. 2017). For effective monitoring,  
480 collaborations between researchers appear to be a powerful way to efficiently improve  
481 specialised and general knowledge in the long term (Høye and Culler 2018), e.g. through the  
482 formalisation of standardised study protocols (e.g. Moretti et al. 2017) or by building global  
483 databases on spider traits (e.g. Pekár et al. 2021).

484

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493

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792 **TABLE**

793 *Table 1*

794 Generalized linear models (GLM) with Poisson or Negative Binomial (NB) distributions, and  
795 linear models (LM) performed to test the effect of habitat (H) and elevation (E) on the mother  
796 carapace width (CW) or on clutch size (CS), and comparisons using Anova type II. The  
797 coefficient of determination  $R^2$  is specified for linear models. Not significant interactions  
798 between environmental factors are indicated as "N.S.". The main numbers under the  
799 explanatory variables represent the p-values, in bold when significant (\*) or almost significant  
800 (\*•). The numbers in italics represent (i) either the sum of squares (for LM) or the result of a  
801 likelihood ratio test (for GLM), (ii) the degrees of freedom, and (iii) the F-value (for LM).

802 **FIGURE LEGENDS**

803 *Figure 1*

804 Map of the study area. The light and dark grey dots indicate the location of fen and shrub  
805 plots at high elevation, respectively. The white and black dots indicate the location of fen and  
806 shrub plots at low elevation, respectively. The airport at Narsarsuaq is marked with a white  
807 square. The interval between contour lines is 100 m. The inset indicates where the study area  
808 is located in Greenland. *Modified from Høye et al. (2018).*

809

810 *Figure 2*

811 Mean number of females per pitfall trap according to **a)** habitat type for *Pardosa furcifera*,  
812 and **b)** habitat type and elevation for *P. hyperborea*, in Narsarsuaq between 2015 and 2017.  
813 The bars represent the standard error, statistically different means do not share letters, and the  
814 number of observations is given in italics.

815

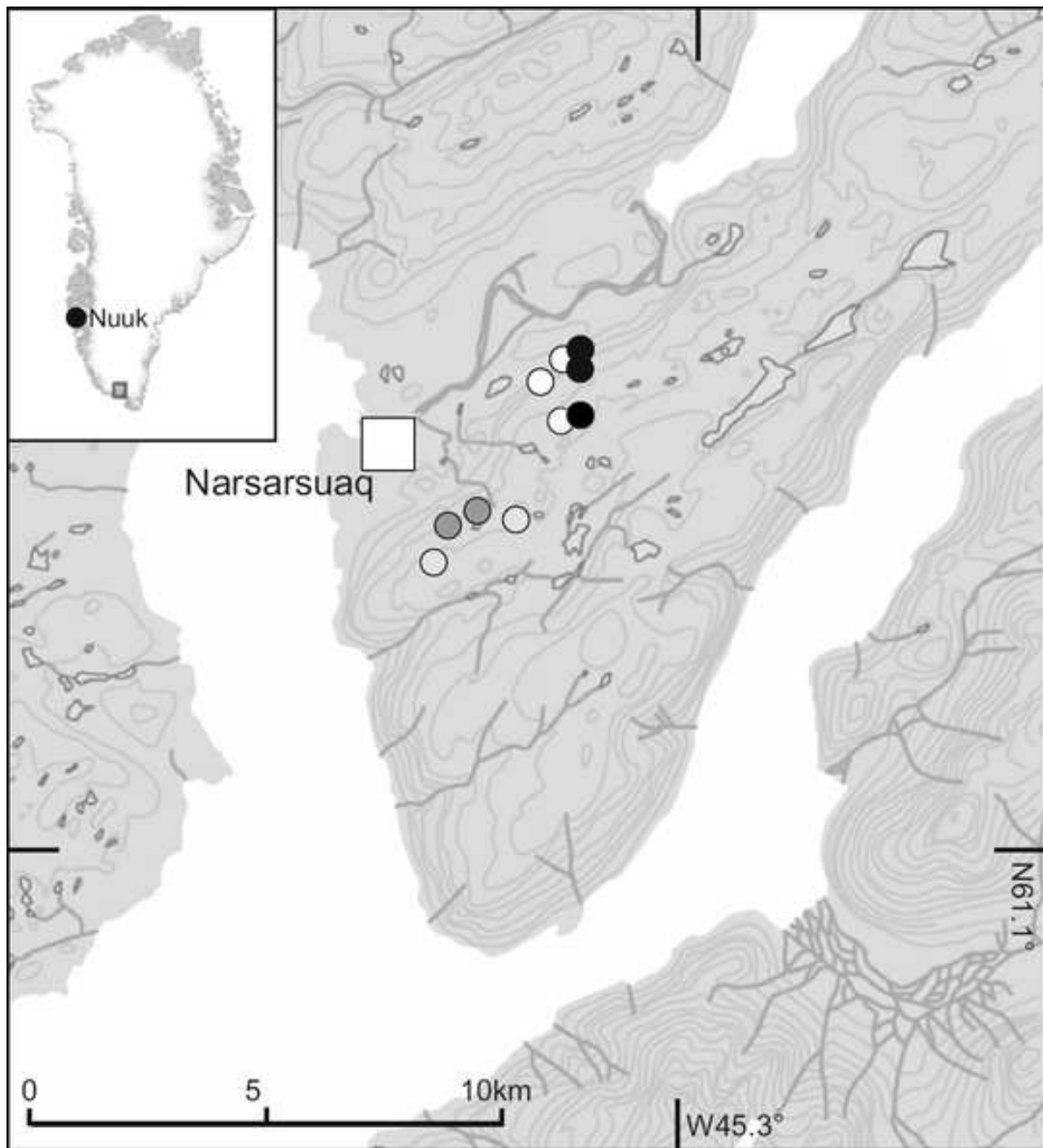
816 *Figure 3*

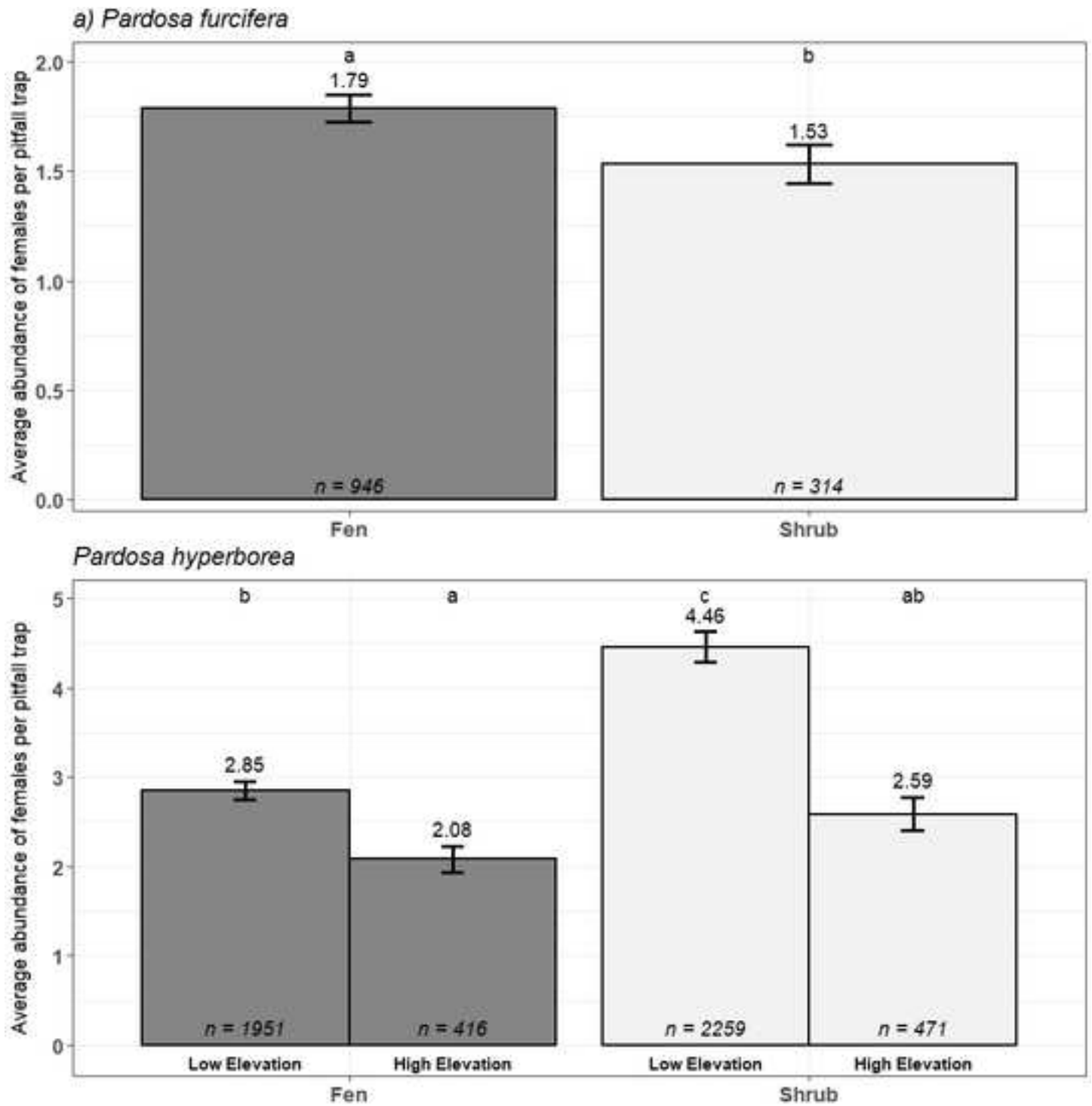
817 Negative Binomial Regressions between the number of eggs per cocoon and the carapace  
818 width (CW) of females in millimetres (mm) for *Pardosa furcifera* (triangle shape in black)  
819 and for *P. hyperborea* (round dots in dark grey), in Narsarsuaq (data from 2015 to 2017  
820 pooled together).

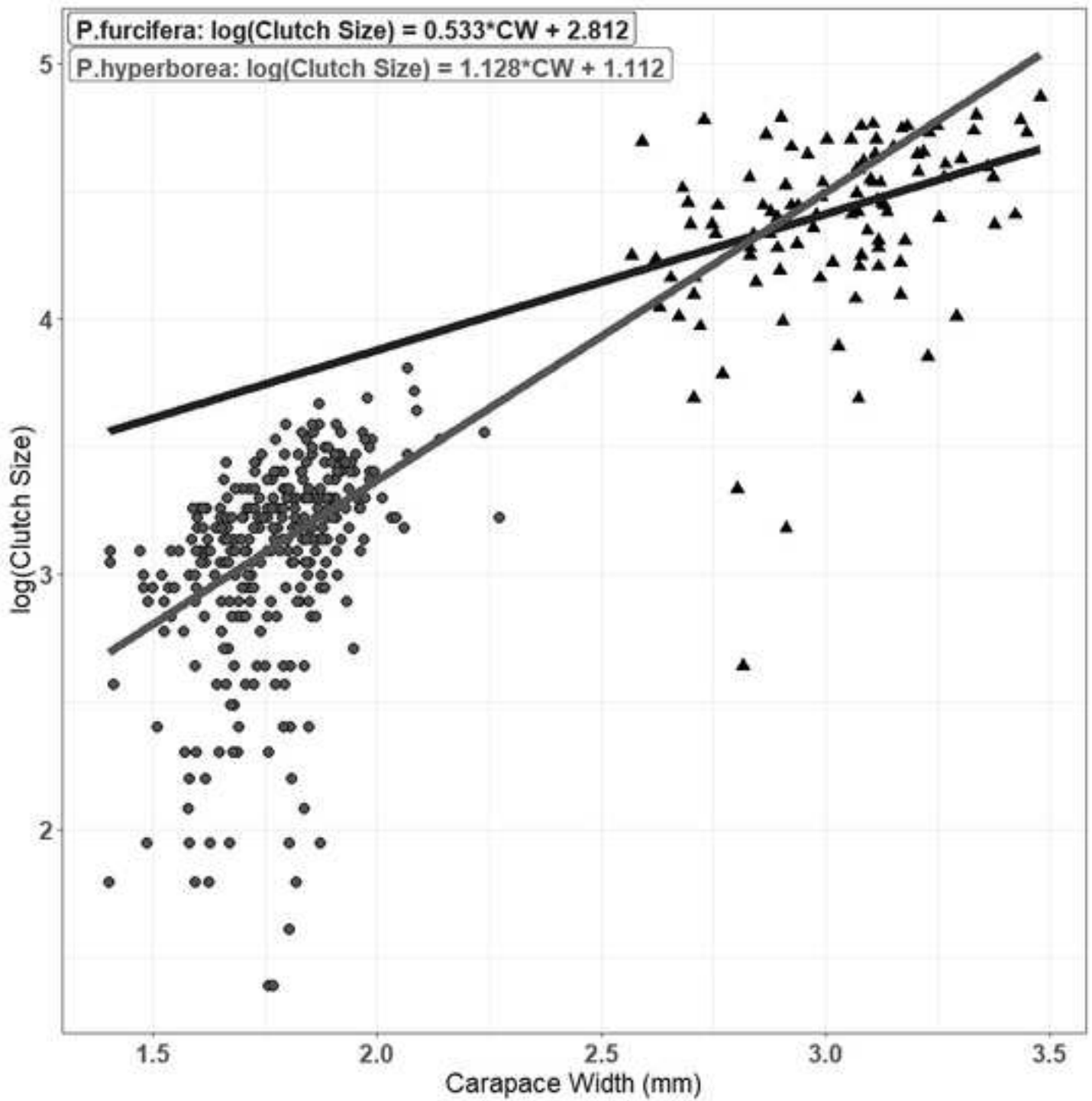
821

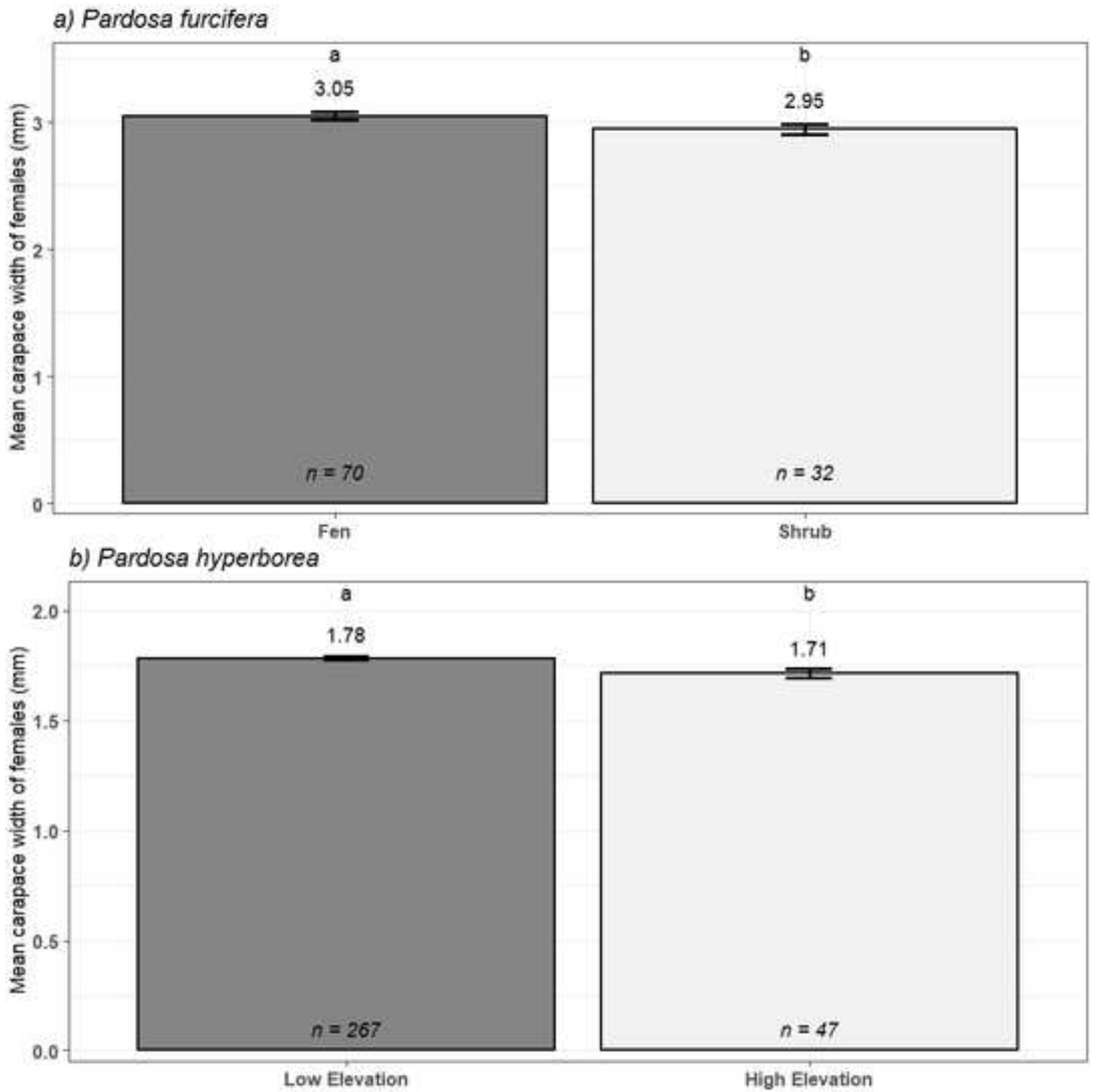
822 *Figure 4*

823 Mean carapace width of females in millimeters (mm) according to **a**) habitat for *Pardosa*  
824 *furcifera*, and **b**) elevation for *P. hyperborea* in Narsarsuaq (data from 2015 to 2017 pooled  
825 together). The bars represent the standard error, statistically different means do not share  
826 letters, and the number of observations is given in italics.



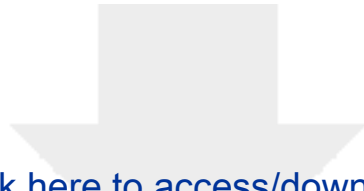






Response Variable	Species	Model (distribution)	R <sup>2</sup>	Explanatory Variables
	Habitat	Elevation	CW	Interaction
Abundance	<i>P. furcifera</i>	GLM (Poisson)	"0.0172 *	
5.67 1"	"0.2802			
1.17 1"	N.S.			
Abundance	<i>P. hyperborea</i>	GLM (NB)	"<0.0001 *	
75.1 1"	"<0.0001 *			
56.3 1"	"0.0428 *			
4.10 1"				
Clutch Size	<i>P. furcifera</i>	GLM (NB)		"<0.0001 *
17.14 1"				
Clutch Size	<i>P. hyperborea</i>	GLM (NB)		"<0.0001 *
89.33 1"				
Body Size	<i>P. furcifera</i>	LM	0.0477	"0.0287 *
0.22 1 4.92"	" 0.6935			
0.01 1 0.16"	N.S.			
Body Size	<i>P. hyperborea</i>	LM	0.0331	"0.7779
0.001 1 0.08"	"0.0013 *			
0.20 1 10.58"	N.S.			
Clutch Size	<i>P. furcifera</i>	GLM (NB)		"0.9158
0.01 1"	"0.0551•			
3.68 1"	"<0.0001 *			
17.42 1"	N.S.			
Clutch Size	<i>P. hyperborea</i>	GLM (NB)		"0.2495
1.33 1"	"0.2287			
1.45 1"	"<0.0001 *			
83.85 1"	N.S.			

Response Variable	Species	Model (distribution)	R <sup>2</sup>	Explanatory Variables			
				Habitat	Elevation	CW	Interaction
Abundance	<i>P. furcifera</i>	GLM (Poisson)		<b>0.0172 *</b> 5.67/1	0.2802 1.17/1		N.S.
Abundance	<i>P. hyperborea</i>	GLM (NB)		<b>&lt;0.0001 *</b> 75.1/1	<b>&lt;0.0001 *</b> 56.3/1		<b>0.0428 *</b> 4.10/1
Clutch Size	<i>P. furcifera</i>	GLM (NB)				<b>&lt;0.0001 *</b> 17.14/1	
Clutch Size	<i>P. hyperborea</i>	GLM (NB)				<b>&lt;0.0001 *</b> 89.33/1	
Body Size	<i>P. furcifera</i>	LM	0.0477	<b>0.0287 *</b> 0.22/1/4.92	0.6935 0.01/1/0.16		N.S.
Body Size	<i>P. hyperborea</i>	LM	0.0331	0.7779 0.001/1/0.08	<b>0.0013 *</b> 0.20/1/10.58		N.S.
Clutch Size	<i>P. furcifera</i>	GLM (NB)		0.9158 0.01/1	<b>0.0551 •</b> 3.68/1	<b>&lt;0.0001 *</b> 17.42/1	N.S.
Clutch Size	<i>P. hyperborea</i>	GLM (NB)		0.2495 1.33/1	0.2287 1.45/1	<b>&lt;0.0001 *</b> 83.85/1	N.S.



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