



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

Nathan Viel, Cecilie Mielec, Julien Petillon, Toke T. Hoye

## ► To cite this version:

Nathan Viel, Cecilie Mielec, Julien Petillon, Toke T. Hoye. Variation in abundance and life-history traits of two congeneric Arctic wolf spider species, *Pardosa hyperborea* and *Pardosa furcifera*, along local environmental gradients. *Polar Biology*, 2022, 45 (5), pp.937-950. 10.1007/s00300-022-03041-4 . hal-03657010

**HAL Id: hal-03657010**

**<https://hal.science/hal-03657010>**

Submitted on 9 Sep 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

Nathan Viel<sup>1,2,4,\*</sup>, Cecilie Mielec<sup>2</sup>, Julien Pétillon<sup>1,3,5</sup> and Toke T. Høye<sup>2,6</sup>

<sup>1</sup>Université de Rennes, UMR CNRS 6553 Ecobio, 35000 Rennes, France

<sup>2</sup>Aarhus University, Department of Ecoscience and Arctic Research Centre, C. F. Møllers Allé  
48, 8000 Aarhus, Denmark

<sup>3</sup>Nelson Mandela University, Institute for Coastal and Marine Research, Port Elizabeth 6031,  
South Africa

<sup>4</sup><https://orcid.org/0000-0002-2915-8464>

<sup>5</sup><https://orcid.org/0000-0002-7611-5133>

<sup>6</sup><https://orcid.org/0000-0001-5387-3284>

\*Corresponding author; Email: [pro.viel.nathan@gmail.com](mailto:pro.viel.nathan@gmail.com)

## ABSTRACT

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

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

## DECLARATIONS

**Funding:** An Erasmus+ grant allowed NV to complete an internship, as part of a master's degree, which led to the writing of this manuscript. Travel from University of Rennes 1 to Aarhus University was funded by ECOBIO (UR1).

**Conflicts of interest/Competing interests:** The authors declare that they have no conflict of interest.

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

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

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

## INTRODUCTION

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

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

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

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

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

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

## MATERIALS AND METHODS

### *Studied species*

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

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



## Study area and experimental design

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

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

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

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

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

### *Laboratory work*

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

### *Statistics*

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

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

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

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

## RESULTS

### *Abundances*

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

### *Body size and fecundity*

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

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

## DISCUSSION

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

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

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

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

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

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

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

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

### *Body size*

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

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



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

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

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

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

### *Fecundity*

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

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

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

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

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

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

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

## ACKNOWLEDGEMENTS

We would like to thank ECOBIO from the University of Rennes 1 (UR1) and the Arctic Research Centre (ARC) from Aarhus University (AU) for supporting this project. We thank the Natural History Museum Aarhus for the use of laboratory facilities and the storage of samples. NV acknowledges funding from Erasmus+ program and financial support from ECOBIO which allowed the fulfilment of this project. TTH thanks numerous field assistants for help with fieldwork over the years. We also thank Seppo Koponen and an anonymous reviewer for their valuable feedback on this manuscript.

## REFERENCES

- Ahrens L, Kraus JM (2006) Wolf spider (Araneae, Lycosidae) movement along a pond edge. *J Arachnol* 34:532–539. <https://doi.org/10.1636/05-85.1>
- Ameline C, Puzin C, Bowden JJ, et al (2017) Habitat specialization and climate affect arthropod fitness: a comparison of generalist vs. specialist spider species in Arctic and temperate biomes. *Biol J Linn Soc* 121:592–599. <https://doi.org/10.1093/biolinnean/blx014>

Ameline C, Høye TT, Bowden JJ, et al (2018) Elevational variation of body size and reproductive traits in high-latitude wolf spiders (Araneae: Lycosidae). *Polar Biol* 41:2561–2574. <https://doi.org/10.1007/s00300-018-2391-5>

Bartomeus I, Gravel D, Tylianakis JM, et al (2016) A common framework for identifying linkage rules across different types of interactions. *Funct Ecol* 30:1894–1903. <https://doi.org/10.1111/1365-2435.12666>

Beckers N, Hein N, Vanselow KA, Löffler J (2018) Effects of Microclimatic Thresholds on the Activity-Abundance and Distribution Patterns of Alpine Carabidae Species. *Ann Zool Fenn* 55:25–44. <https://doi.org/10.5735/086.055.0104>

Beckers N, Hein N, Anneser A, et al (2020) Differences in Mobility and Dispersal Capacity Determine Body Size Clines in Two Common Alpine-Tundra Arthropods. *Insects* 11:74. <https://doi.org/10.3390/insects11020074>

Berry AD, Culbertson KM, Rypstra AL (2018) Comparative reproductive output of two cellar spiders (Pholcidae) that coexist in southwest Ohio. *J Arachnol* 46:549–552. <https://doi.org/10.1636/JoA-S-18-007.1>

Blanckenhorn WU (1997) Altitudinal life history variation in the dung flies *Scathophaga stercoraria* and *Sepsis cynipsea*. *Oecologia* 109:342–352. <https://doi.org/10.1007/s004420050092>

Blanckenhorn WU, Demont M (2004) Bergmann and Converse Bergmann Latitudinal Clines in Arthropods: Two Ends of a Continuum? *Integr Comp Biol* 44:413–424. <https://doi.org/10.1093/icb/44.6.413>

Böcher J, Kristensen NP, Pape T, Vilhelmsen L (eds) (2015) The Greenland entomofauna: an identification manual of insects, spiders and their allies. Brill, Leiden Boston

Bonfanti J, Hedde M, Joimel S, et al (2018) Intraspecific body size variability in soil organisms at a European scale: Implications for functional biogeography. *Funct Ecol* 32:2562–2570. <https://doi.org/10.1111/1365-2435.13194>

Bowden JJ, Buddle CM (2010) Spider Assemblages across Elevational and Latitudinal Gradients in the Yukon Territory, Canada. *Arctic* 63:261–272. <https://doi.org/10.14430/arctic1490>

Bowden JJ, Buddle CM (2012) Life history of tundra-dwelling wolf spiders (Araneae: Lycosidae) from the Yukon Territory, Canada. *Can J Zool* 90:714–721. <https://doi.org/10.1139/z2012-038>

Bowden JJ, Høye TT, Buddle CM (2013) Fecundity and sexual size dimorphism of wolf spiders (Araneae: Lycosidae) along an elevational gradient in the Arctic. *Polar Biol* 36:831–836. <https://doi.org/10.1007/s00300-013-1308-6>

Bowden JJ, Hansen RR, Olsen K, Høye TT (2015) Habitat-specific effects of climate change on a low-mobility Arctic spider species. *Polar Biol* 38:559–568. <https://doi.org/10.1007/s00300-014-1622-7>

- 538 Bowden JJ, Hansen OLP, Olsen K, et al (2018) Drivers of inter-annual variation and long-term  
539 change in High-Arctic spider species abundances. *Polar Biol* 41:1635–1649.  
540 <https://doi.org/10.1007/s00300-018-2351-0>
- 541 Brown JH, Gillooly JF, Allen AP, et al (2004) Toward a metabolic theory of Ecology. *Ecology*  
542 85:1771–1789. <https://doi.org/10.1890/03-9000>
- 543 Buddle CM (2000) Life History of *Pardosa moesta* and *Pardosa mackenziana* (Araneae,  
544 Lycosidae) in Central Alberta, Canada. *J Arachnol* 28:319–328.  
545 [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)
- 546 CAFF (2013) Arctic biodiversity assessment. Status and trends in arctic biodiversity.  
547 Conservation of Arctic Flora and Fauna, Akureyri
- 548 Chown SL, Gaston KJ (1999) Exploring links between physiology and ecology at macro-scales:  
549 the role of respiratory metabolism in insects. *Biol Rev* 74:87–120
- 550 Chown SL, Klok CJ (2003) Altitudinal body size clines: latitudinal effects associated with  
551 changing seasonality. *Ecography* 26:445–455. <https://doi.org/10.1034/j.1600-0587.2003.03479.x>
- 553 Dahl MT, Yoccoz NG, Aakra K, Coulson SJ (2018) The Araneae of Svalbard: the relationships  
554 between specific environmental factors and spider assemblages in the High Arctic. *Polar Biol* 41:839–853. <https://doi.org/10.1007/s00300-017-2247-4>
- 556 Dearn JM (1977) Variable life history characteristics along an altitudinal gradient in three  
557 species of Australian grasshopper. *Oecologia* 28:67–85.  
558 <https://doi.org/10.1007/BF00346837>
- 559 Deevey GB (1949) The Developmental History of *Latrodectus Mactans* (Fabr.) at Different  
560 Rates of Feeding. *Am Midl Nat* 42:189. <https://doi.org/10.2307/2421795>
- 561 DeVito J, Meik JM, Gerson MM, Formanowicz, Jr. DR (2004) Physiological tolerances of three  
562 sympatric riparian wolf spiders (Araneae: Lycosidae) correspond with microhabitat  
563 distributions. *Can J Zool* 82:1119–1125. <https://doi.org/10.1139/z04-090>
- 564 Dondale CD, Redner JH (1990) The wolf spiders, nurseryweb spiders, and lynx spiders of  
565 Canada and Alaska: Araneae: Lycosidae, Pisauridae, and Oxyopidae. In: *The Insects and arachnids of Canada*. Research Branch, Agriculture Canada, Ottawa
- 567 Eberhard WG (1979) Rates of Egg Production by Tropical Spiders in the Field. *Biotropica*  
568 11:292–300. <https://doi.org/10.2307/2387921>
- 569 Edgar WD (1972) The life-cycle of the Wolf spider *Pardosa lugubris* in Holland. *J Zool* 168:1–  
570 7. <https://doi.org/10.1111/j.1469-7998.1972.tb01336.x>
- 571 Eitzinger B, Abrego N, Gravel D, et al (2019) Assessing changes in arthropod predator–prey  
572 interactions through DNA- based gut content analysis—variable environment, stable  
573 diet. *Mol Ecol* 28:266–280. <https://doi.org/10.1111/mec.14872>
- 574 Foelix RF (2011) *Biology of spiders*, 3rd ed. Oxford University Press, Oxford New York



- 575 Fox CW, Czesak ME (2000) Evolutionary Ecology of Progeny Size in Arthropods. *Annu Rev*  
576 *Entomol* 45:341–369. <https://doi.org/10.1146/annurev.ento.45.1.341>
- 577 Fox J, Weisberg S (2019) *An R Companion to Applied Regression*, Third. Sage, Thousand  
578 Oaks CA
- 579 Frick H, Kropf C, Nentwig W (2007) Laboratory Temperature Preferences of the Wolf Spider  
580 *Pardosa riparia* (Araneae: Lycosidae). *Arachnology* 14:45–48.  
581 <https://doi.org/10.13156/arac.2007.14.1.45>
- 582 Frost GV, Epstein HE, Walker DA, et al (2013) Patterned-ground facilitates shrub expansion  
583 in Low Arctic tundra. *Environ Res Lett* 8:015035. [https://doi.org/10.1088/1748-](https://doi.org/10.1088/1748-9326/8/1/015035)  
584 [9326/8/1/015035](https://doi.org/10.1088/1748-9326/8/1/015035)
- 585 García LF, Viera C, Pekár S (2018) Comparison of the capture efficiency, prey processing, and  
586 nutrient extraction in a generalist and a specialist spider predator. *Sci Nat* 105:1–10
- 587 Greenstone MH (1984) Determinants of web spider species diversity: Vegetation structural  
588 diversity vs. prey availability. *Oecologia* 62:299–304.  
589 <https://doi.org/10.1007/BF00384260>
- 590 Hagstrum DW (1971) Carapace Width as a Tool for Evaluating the Rate of Development of  
591 Spiders in the Laboratory and the Field1. *Ann Entomol Soc Am* 64:757–760.  
592 <https://doi.org/10.1093/aesa/64.4.757>
- 593 Halsch CA, Shapiro AM, Fordyce JA, et al (2021) Insects and recent climate change. *Proc Natl*  
594 *Acad Sci* 118:e2002543117. <https://doi.org/10.1073/pnas.2002543117>
- 595 Hansen RR, Hansen OLP, Bowden JJ, et al (2016) Meter scale variation in shrub dominance  
596 and soil moisture structure Arctic arthropod communities. *PeerJ* 4:e2224.  
597 <https://doi.org/10.7717/peerj.2224>
- 598 Hein N, Feilhauer H, Finch O-D, et al (2014) Snow cover determines the ecology and  
599 biogeography of spiders (Araneae) in alpine tundra ecosystems. *Erdkunde* 63:157–172.  
600 <https://doi.org/10.3112/erdkunde.2014.03.01>
- 601 Hein N, Brendel MR, Feilhauer H, et al (2018) Egg size versus egg number trade-off in the  
602 alpine-tundra wolf spider, *Pardosa palustris* (Araneae: Lycosidae). *Polar Biol* 41:1607–  
603 1617. <https://doi.org/10.1007/s00300-018-2301-x>
- 604 Hein N, Löffler J, Feilhauer H (2019a) Mapping of arthropod alpha and beta diversity in  
605 heterogeneous arctic-alpine ecosystems. *Ecol Inform* 54:101007.  
606 <https://doi.org/10.1016/j.ecoinf.2019.101007>
- 607 Hein N, Pétilion J, Pape R, et al (2019b) Broad-scale rather than fine-scale environmental  
608 variation drives body size in a wandering predator (Araneae, Lycosidae). *Arct Antarct*  
609 *Alp Res* 51:315–326. <https://doi.org/10.1080/15230430.2019.1640039>
- 610 Hendrickx F, Maelfait J-P (2003) Life cycle, reproductive patterns and their year-to-year  
611 variation in a field population of the wolf spider *Pirata piraticus* (Araneae, Lycosidae).  
612 *J Arachnol* 31:331–339. <https://doi.org/10.1636/m01-98>

613 Hervé M (2019) RVAideMemoire: Testing and Plotting Procedures for Biostatistics

614 Hobbie JE, Shaver GR, Rastetter EB, et al (2017) Ecosystem responses to climate change at a  
 615 Low Arctic and a High Arctic long-term research site. *Ambio* 46:160–173.  
 616 <https://doi.org/10.1007/s13280-016-0870-x>

617 Hobbie J, Shaver G, Høye TT, Bowden J (2021) Arctic Tundra.  
 618 <https://doi.org/10.1002/9781118846582.ch5>. In: Thomas DN (Ed.) *Arctic Ecology*.  
 619 John Wiley & Sons, Ltd, pp 103–132

620 Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community  
 621 responses to altitude. *Biol Rev* 80:489. <https://doi.org/10.1017/S1464793105006767>

622 Hodkinson ID (2018) Insect Biodiversity in the Arctic. In: *Insect Biodiversity*. John Wiley &  
 623 Sons, Ltd, Chichester, UK, pp 15–57

624 Horne CR, Hirst AG, Atkinson D (2015) Temperature-size responses match latitudinal-size  
 625 clines in arthropods, revealing critical differences between aquatic and terrestrial  
 626 species. *Ecol Lett* 18:327–335. <https://doi.org/10.1111/ele.12413>

627 Høye TT (2020) Arthropods and climate change – arctic challenges and opportunities. *Curr*  
 628 *Opin Insect Sci* 41:40–45. <https://doi.org/10.1016/j.cois.2020.06.002>

629 Høye TT, Culler LE (2018) Tundra arthropods provide key insights into ecological responses  
 630 to environmental change. *Polar Biol* 41:1523–1529. <https://doi.org/10.1007/s00300-018-2370-x>  
 631

632 Høye TT, Hammel J (2010) Climate change and altitudinal variation in sexual size dimorphism  
 633 of arctic wolf spiders. *Clim Res* 41:259–265. <https://doi.org/10.3354/cr00855>

634 Høye TT, Hammel JU, Fuchs T, Toft S (2009) Climate change and sexual size dimorphism in  
 635 an Arctic spider. *Biol Lett* 5:542–544. <https://doi.org/10.1098/rsbl.2009.0169>

636 Høye TT, Bowden JJ, Hansen OLP, et al (2018) Elevation modulates how Arctic arthropod  
 637 communities are structured along local environmental gradients. *Polar Biol* 41:1555–  
 638 1565. <https://doi.org/10.1007/s00300-017-2204-2>

639 Høye TT, Loboda S, Koltz AM, et al (2020) Taxonomic, temporal, and spatial variation in the  
 640 dynamics of High-Arctic arthropod populations. *bioRxiv* 2020.04.27.052795.  
 641 <https://doi.org/10.1101/2020.04.27.052795>

642 Høye TT, Loboda S, Koltz AM, et al (2021) Nonlinear trends in abundance and diversity and  
 643 complex responses to climate change in Arctic arthropods. *Proc Natl Acad Sci*  
 644 118:e2002557117. <https://doi.org/10.1073/pnas.2002557117>

645 IPCC (2019) Climate Change and Land: an IPCC special report on climate change,  
 646 desertification, land degradation, sustainable land management, food security, and  
 647 greenhouse gas fluxes in terrestrial ecosystems. In: Shukla PR, Skea J, Calvo Buendia  
 648 E, Masson-Delmotte V, Pörtner H-O, Roberts DC, Zhai P, Slade R, Connors S, van  
 649 Diemen R, Ferrat M, Haughey E, Luz S, Neogi S, Pathak M, Petzold J, Portugal Pereira  
 650 J, Vyas P, Huntley E, Kissick K, Belkacemi M, Malley J (eds) In press

651 Jakob EM, Marshall SD, Uetz GW (1996) Estimating Fitness: A Comparison of Body  
652 Condition Indices. *Oikos* 77:61–67. <https://doi.org/10.2307/3545585>

653 Jocqué R, Alderweireldt M (2005) Lycosidae: the grassland spiders. *Acta Zool Bulg* 1:125–130

654 Killebrew DW, Ford NB (1985) Reproductive tactics and female body size in the green lynx  
655 spider, *Peucetia viridans* (Araneae, Oxyopidae). *J Arachnol* 13:375–382

656 Kingsolver JG (1983) Ecological Significance of Flight Activity in *Colias* Butterflies:  
657 Implications for Reproductive Strategy and Population Structure. *Ecology* 64:546–551.  
658 <https://doi.org/10.2307/1939974>

659 Kingsolver JG, Huey RB (2008) Size, temperature, and fitness: three rules. *Evol Ecol Res*  
660 10:251–268

661 Kiss B, Samu F (2000) Evaluation of population densities of the common wolf spider *Pardosa*  
662 *agrestis* (Araneae: Lycosidae) in Hungarian alfalfa fields using mark-recapture. *Eur J*  
663 *Entomol* 97:191–195. <https://doi.org/10.14411/eje.2000.036>

664 Koltz AM, Wright JP (2020) Impacts of female body size on cannibalism and juvenile  
665 abundance in a dominant arctic spider. *J Anim Ecol* 89:1788–1798.  
666 <https://doi.org/10.1111/1365-2656.13230>

667 Koltz AM, Schmidt NM, Høye TT (2018) Differential arthropod responses to warming are  
668 altering the structure of Arctic communities. *R Soc Open Sci* 5:171503.  
669 <https://doi.org/10.1098/rsos.171503>

670 Körner C (2007) The use of ‘altitude’ in ecological research. *Trends Ecol Evol* 22:569–574.  
671 <https://doi.org/10.1016/j.tree.2007.09.006>

672 Lee JE, Somers MJ, Chown SL (2012) Density, body size and sex ratio of an indigenous spider  
673 along an altitudinal gradient in the sub-Antarctic. *Antarct Sci* 24:15–22.  
674 <https://doi.org/10.1017/S0954102011000629>

675 Legault G, Weis AE (2013) The impact of snow accumulation on a heath spider community in  
676 a sub-Arctic landscape. *Polar Biol* 36:885–894. <https://doi.org/10.1007/s00300-013-1313-9>

678 Lenth R (2019) emmeans: Estimated Marginal Means, aka Least-Squares Means

679 Loboda S, Savage J, Buddle CM, et al (2018) Declining diversity and abundance of High Arctic  
680 fly assemblages over two decades of rapid climate warming. *Ecography* 41:265–277.  
681 <https://doi.org/10.1111/ecog.02747>

682 Mammola S, Milano F, Vignal M, et al (2019) Associations between habitat quality, body size  
683 and reproductive fitness in the alpine endemic spider *Vesubia jugorum*. *Glob Ecol*  
684 *Biogeogr* 28:1325–1335. <https://doi.org/10.1111/geb.12935>

685 Marshall SD, Gittleman JL (1994) Clutch size in spiders: is more better? *Funct Ecol* 8:118–  
686 124. <https://doi.org/10.2307/2390120>

- 687 Marshall SD, Rypstra AL (1999) Spider competition in structurally simple ecosystems. J  
688 Arachnol 343–350
- 689 Marusik YM (2015) Araneae (Spiders). In: Böcher J, Kristensen NP, Pape T, Vilhelmsen L  
690 (eds) The Greenland entomofauna: an identification manual of insects, spiders and their  
691 allies. Brill, Leiden Boston, pp 667–703
- 692 Marusik YM, Koponen S (2002) Diversity of spiders in Boreal and Arctic zones. J Arachnol  
693 30:205–210. [https://doi.org/10.1636/0161-8202\(2002\)030\[0205:DOSIBA\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2002)030[0205:DOSIBA]2.0.CO;2)
- 694 McNab BK (1971) On the Ecological Significance of Bergmann's Rule. Ecology 52:845–854.  
695 <https://doi.org/10.2307/1936032>
- 696 Meiri S, Dayan T (2003) On the validity of Bergmann's rule. J Biogeogr 30:331–351.  
697 <https://doi.org/10.1046/j.1365-2699.2003.00837.x>
- 698 Miyashita K (1968) Growth and development of *Lycosa T-insignita* Boes. et Str.(Araneae:  
699 Lycosidae) under different feeding conditions. Appl Entomol Zool 3:81–88
- 700 Monsimet J, Colinet H, Devineau O, et al (2021) Biogeographic position and body size jointly  
701 set lower thermal limits of wandering spiders. Ecol Evol 11:3347–3356.  
702 <https://doi.org/10.1002/ece3.7286>
- 703 Moretti M, Dias ATC, Bello F, et al (2017) Handbook of protocols for standardized  
704 measurement of terrestrial invertebrate functional traits. Funct Ecol 31:558–567.  
705 <https://doi.org/10.1111/1365-2435.12776>
- 706 Morse DH (1997) Distribution, movement, and activity patterns of an intertidal wolf spider  
707 *Pardosa lapidicina* population (Araneae, Lycosidae). J Arachnol 25:1–10
- 708 Nentwig W, Blick T, Gloor D, et al (2021) Spiders of Europe. <https://araneae.nmbe.ch/>.  
709 Accessed 14 Apr 2021
- 710 Oliver T, Hill JK, Thomas CD, et al (2009) Changes in habitat specificity of species at their  
711 climatic range boundaries. Ecol Lett 12:1091–1102. <https://doi.org/10.1111/j.1461-0248.2009.01367.x>
- 713 Otto C, Svensson BS (1982) Structure of communities of ground-living spiders along altitudinal  
714 gradients. Ecography 5:35–47. <https://doi.org/10.1111/j.1600-0587.1982.tb01015.x>
- 715 Paquin P, Dupérré N (2003) Guide d'identification des araignées (Araneae) du Québec,  
716 Association des entomologistes amateurs du Québec. Fabriques, Supplément 11,  
717 Varennes
- 718 Pekár S, Vaňhara P (2006) Geographical sexual size dimorphism in an ant- eating spider,  
719 *Zodarium rubidum* (Araneae: Zodariidae). J Nat Hist 40:1343–1350.  
720 <https://doi.org/10.1080/00222930600901417>
- 721 Pekár S, Wolff JO, Černecká L, et al (2021) The World Spider Trait database: a centralized  
722 global open repository for curated data on spider traits. Database 2021:baab064.  
723 <https://doi.org/10.1093/database/baab064>

- 724 Petersen B (1950) The relation between size of mother and number of eggs and young in some  
725 spiders and its significance for the evolution of size. *Experientia* 6:96–98.  
726 <https://doi.org/10.1007/BF02153369>
- 727 Pétillon J, Puzin C, Acou A, Outreman Y (2009) Plant invasion phenomenon enhances  
728 reproduction performance in an endangered spider. *Naturwissenschaften* 96:1241–  
729 1246. <https://doi.org/10.1007/s00114-009-0589-7>
- 730 Pétillon J, Lambeets K, Ract-Madoux B, et al (2011) Saline stress tolerance partly matches with  
731 habitat preference in ground-living wolf spiders. *Physiol Entomol* 36:165–172.  
732 <https://doi.org/10.1111/j.1365-3032.2011.00778.x>
- 733 Piacentini LN, Ramírez MJ (2019) Hunting the wolf: A molecular phylogeny of the wolf  
734 spiders (Araneae, Lycosidae). *Mol Phylogenet Evol* 136:227–240.  
735 <https://doi.org/10.1016/j.ympev.2019.04.004>
- 736 Pickavance JR (2001) Life-cycles of four species of *Pardosa* (Araneae, Lycosidae) from the  
737 island of Newfoundland, Canada. *J Arachnol* 29:367–377.  
738 [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)
- 739 Polunin N (1960) Introduction to plant geography and some related sciences, Longmans.  
740 McGraw-Hill, New York
- 741 Punzo F, Farmer C (2006) Life history and ecology of the wolf spider *Pardosa sierra* Banks  
742 (Araneae: Lycosidae) in Southeastern Arizona. *Southwest Nat* 51:310–319.  
743 [https://doi.org/10.1894/0038-4909\(2006\)51\[310:LHAEOT\]2.0.CO;2](https://doi.org/10.1894/0038-4909(2006)51[310:LHAEOT]2.0.CO;2)
- 744 Puzin C, Acou A, Pétillon J, Bonte D (2011) Comparison of reproductive traits between two  
745 salt-marsh wolf spiders (Araneae, Lycosidae) under different habitat suitability  
746 conditions. *Anim Biol* 61:127–138. <https://doi.org/10.1163/157075511X566461>
- 747 R Core Team (2019) R: A language and environment for statistical computing. R Foundation  
748 for Statistical Computing, Vienna, Austria
- 749 Ray C (1960) The application of Bergmann’s and Allen’s rules to the poikilotherms. *J Morphol*  
750 106:85–108. <https://doi.org/10.1002/jmor.1051060104>
- 751 Rich ME, Gough L, Boelman NT (2013) Arctic arthropod assemblages in habitats of differing  
752 shrub dominance. *Ecography* 36:994–1003. <https://doi.org/10.1111/j.1600-0587.2012.00078.x>
- 754 Roff D (1980) Optimizing development time in a seasonal environment: The “ups and downs”  
755 of clinal variation. *Oecologia* 45:202–208. <https://doi.org/10.1007/BF00346461>
- 756 Schmidt NM, Hardwick B, Gilg O, et al (2017) Interaction webs in arctic ecosystems:  
757 Determinants of arctic change? *Ambio* 46:12–25. <https://doi.org/10.1007/s13280-016-0862-x>
- 759 Schmoller R (1970) Life histories of alpine tundra Arachnida in Colorado. *Am Midl Nat* 83:119.  
760 <https://doi.org/10.2307/2424011>

- 761 Simpson MR (1993) Reproduction in two species of arctic arachnids, *Pardosa glacialis* and  
762 *Alopecosa hirtipes*. Can J Zool 71:451–457. <https://doi.org/10.1139/z93-065>
- 763 Simpson MR (1995) Convariation of spider egg and clutch size: the influence of foraging and  
764 parental care. Ecology 76:795–800. <https://doi.org/10.2307/1939345>
- 765 Spiller MS, Spiller C, Garlet J (2017) Arthropod bioindicators of environmental quality. Revista  
766 Agroambiente On-line 12:41. <https://doi.org/10.18227/1982-8470ragro.v12i1.4516>
- 767 Taylor JJ, Lawler JP, Aronsson M, et al (2020) Arctic terrestrial biodiversity status and trends:  
768 A synopsis of science supporting the CBMP State of Arctic Terrestrial Biodiversity  
769 Report. Ambio 49:833–847. <https://doi.org/10.1007/s13280-019-01303-w>
- 770 Venables WN, Ripley BD (2002) Modern Applied Statistics with S, Fourth. Springer, New  
771 York
- 772 Vertainen L, Alatalo RV, Mappes J, Parri S (2000) Sexual differences in growth strategies of  
773 the wolf spider *Hygrolycosa rubrofasciata*. Evol Ecol 14:595–610.  
774 <https://doi.org/10.1023/A:1011080706931>
- 775 Viel N, Mielec C, Pétilion J, Høye TT (2022) Multiple reproductive events in female wolf  
776 spiders *Pardosa hyperborea* and *Pardosa furcifera* in the Low-Arctic: one clutch can hide  
777 another. Polar Biology 45:143–148. <https://doi.org/10.1007/s00300-021-02963-9>
- 778 Violle C, Navas M-L, Vile D, et al (2007) Let the concept of trait be functional! Oikos 116:882–  
779 892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- 780 Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer-Verlag New York
- 781 Wirta HK, Weingartner E, Hambäck PA, Roslin T (2015) Extensive niche overlap among the  
782 dominant arthropod predators of the High Arctic. Basic Appl Ecol 16:86–92.  
783 <https://doi.org/10.1016/j.baae.2014.11.003>
- 784 Wise DH (1975) Food Limitation of the Spider *Linyphia marginata*: Experimental Field  
785 Studies. Ecology 56:637–646. <https://doi.org/10.2307/1935497>
- 786 Wolz M, Klockmann M, Schmitz T, et al (2020) Dispersal and life-history traits in a spider with  
787 rapid range expansion. Mov Ecol 8:1–11. <https://doi.org/10.1186/s40462-019-0182-4>
- 788 Wong MKL, Guénard B, Lewis OT (2019) Trait- based ecology of terrestrial arthropods. Biol  
789 Rev 94:999–1022. <https://doi.org/10.1111/brev.12488>
- 790 Wundram D, Pape R, Löffler J (2010) Alpine Soil Temperature Variability at Multiple Scales.  
791 Arct Antarct Alp Res 42:117–128. <https://doi.org/10.1657/1938-4246-42.1.117>

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).

## FIGURE LEGENDS

### *Figure 1*

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

### *Figure 2*

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

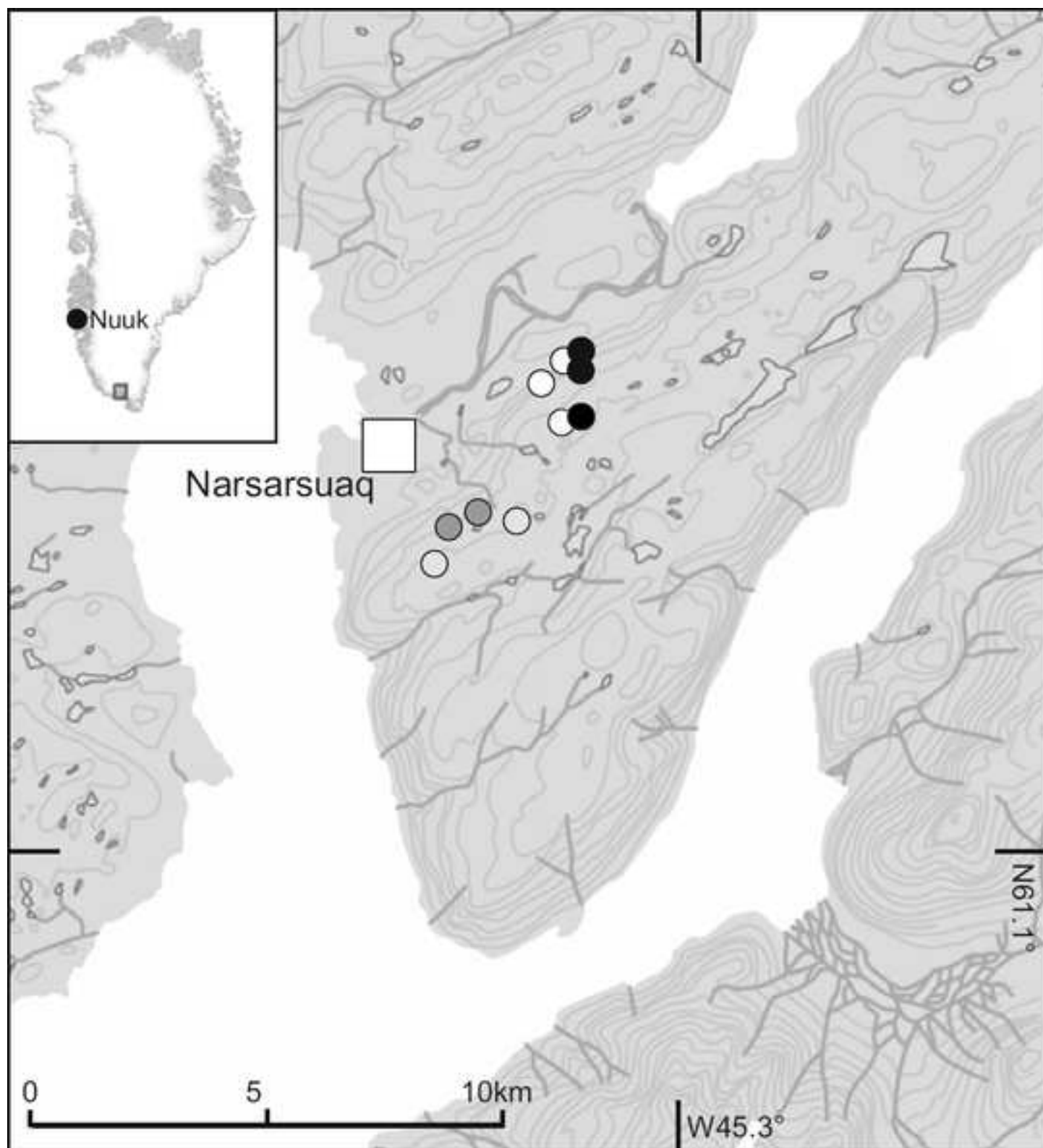
### *Figure 3*

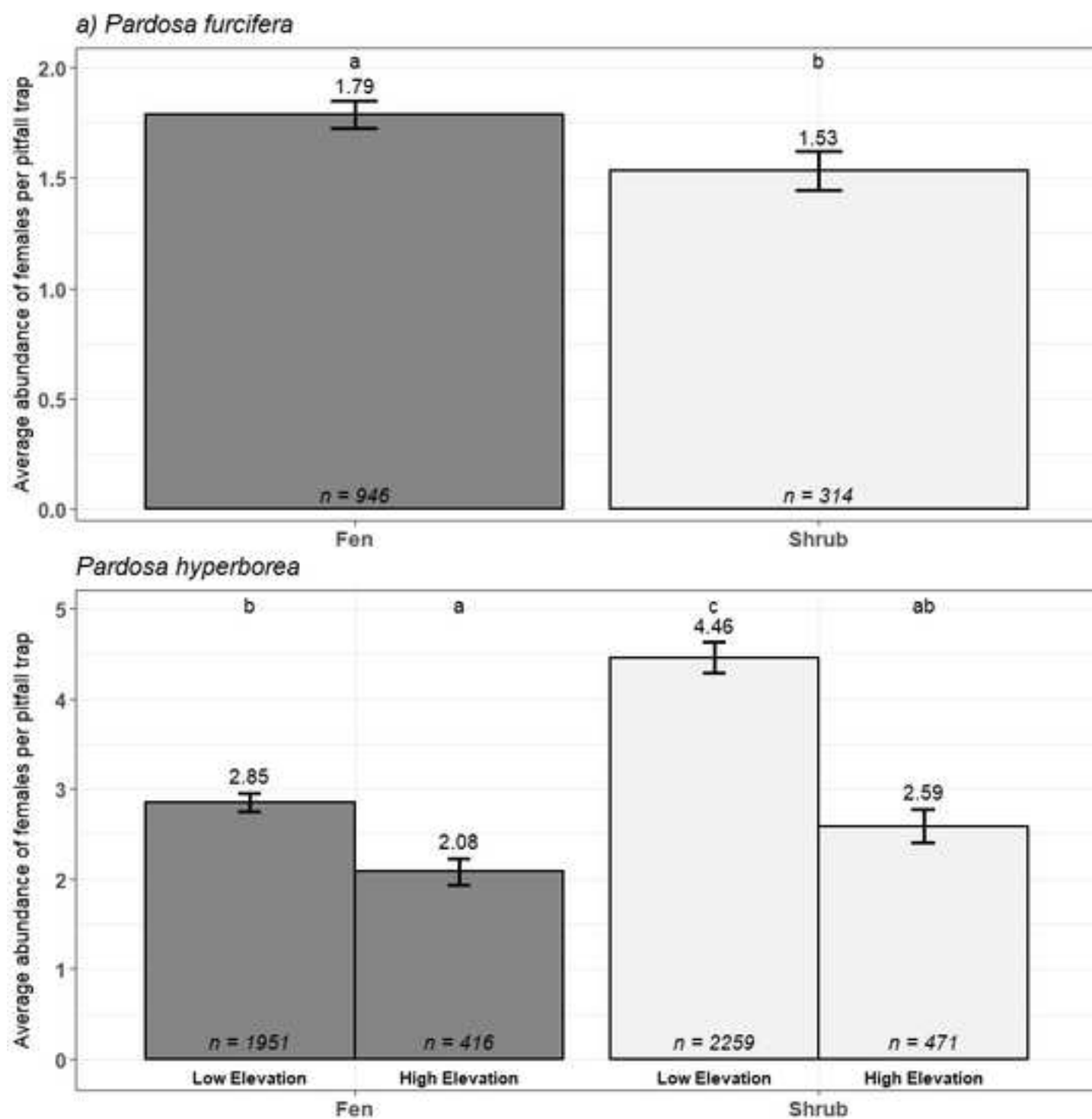
Negative Binomial Regressions between the number of eggs per cocoon and the carapace width (CW) of females in millimetres (mm) for *Pardosa furcifera* (triangle shape in black) and for *P. hyperborea* (round dots in dark grey), in Narsarsuaq (data from 2015 to 2017 pooled together).

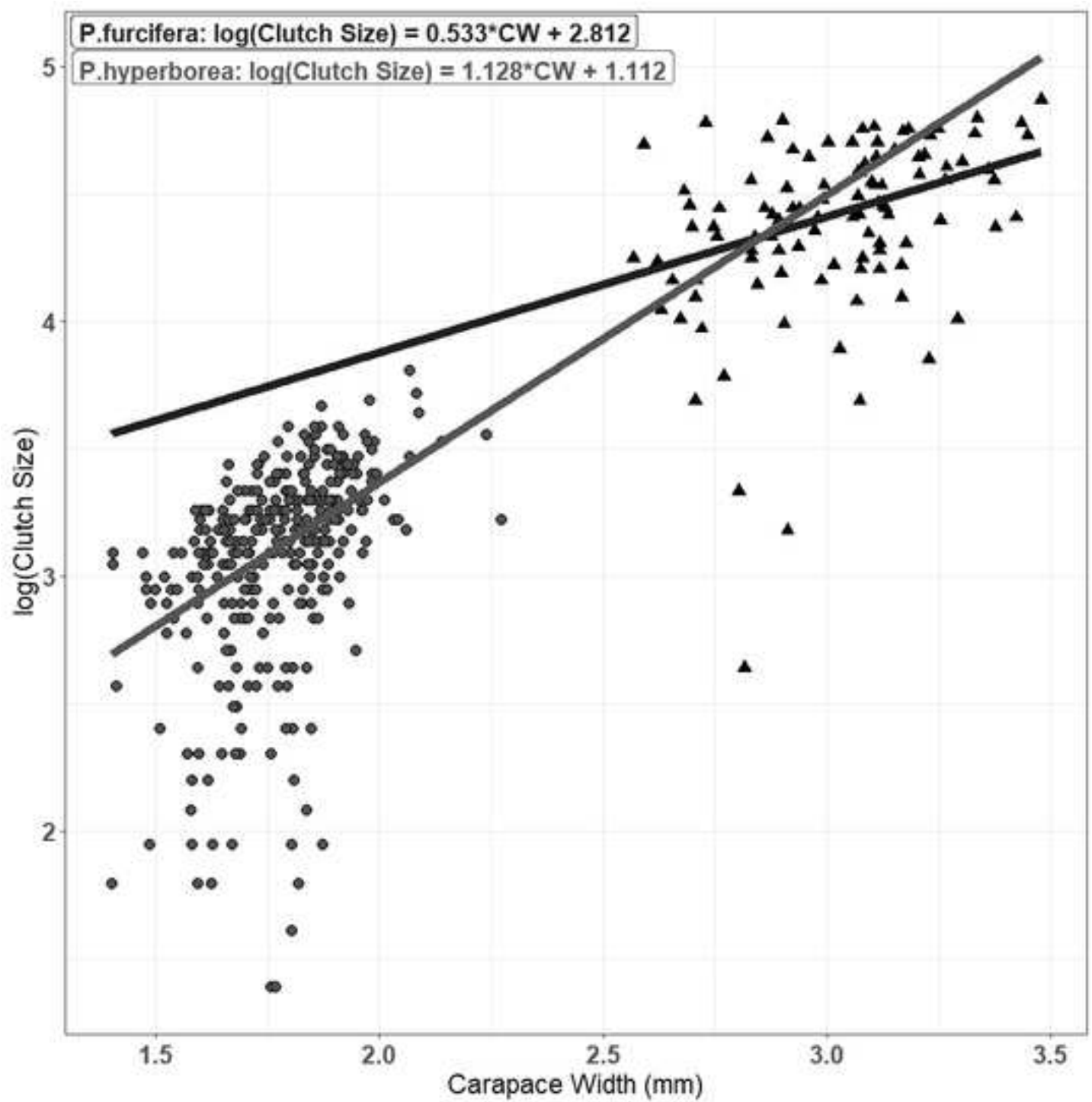
### *Figure 4*

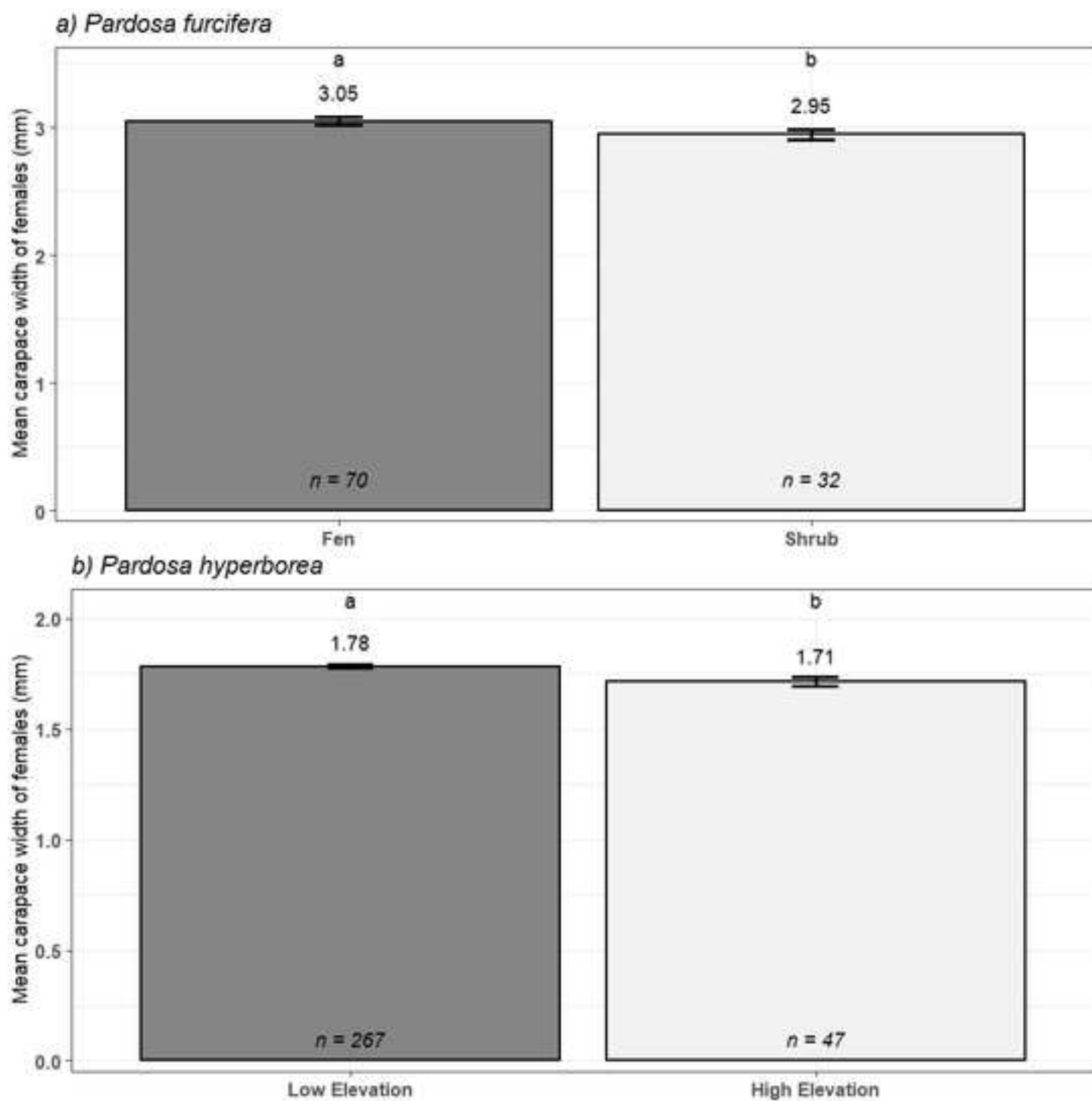


823 Mean carapace width of females in millimeters (mm) according to **a**) habitat for *Pardosa*  
824 *furcifera*, and **b**) elevation for *P. hyperborea* in Narsarsuaq (data from 2015 to 2017 pooled  
825 together). The bars represent the standard error, statistically different means do not share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



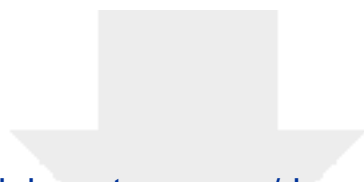






Response Variable	Species	Model (distribution)	R <sup>2</sup>	Explanatory Variables
		Habitat Elevation CW Interaction		
Abundance	<i>P. furcifera</i>	GLM (Poisson)		"0.0172 *
5.67 1"	"0.2802			
1.17 1"	N.S.			
Abundance	<i>P. hyperborea</i>	GLM (NB)		"<0.0001 *
75.1 1"	"<0.0001 *			
56.3 1"	"0.0428 *			
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.



[Click here to access/download](#)

**Electronic Supplementary Material**  
**Variation\_in\_ab\_and\_LHT\_ESM\_1.docx**

