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## Abstract

Environmental gradients can help us comprehend the range of adaptations or plasticity that a given species can exhibit in response to climatic change. In this study, we assessed the response in female body size, clutch size and egg volume to elevational gradients in closely related wolf spiders. We measured these traits in *Pardosa glacialis*, *P. hyperborea*, *P. furcifera* and *P. palustris*, collected along elevational gradients across six sites in Arctic and sub-Arctic regions (four sites in Greenland, one in Iceland and one in the Faroe Islands), although not all species were found at all sites. Body size and reproductive traits did not vary with elevation in a consistent manner among species although smaller species were more sensitive to the gradients. The positive relationship between body size and clutch size was most pronounced in the larger species, indicating that larger species are better able to translate favourable environmental conditions into a larger reproductive output. Our study illustrates that elevational gradients may not fully capture spatial variation in environmental conditions experienced by high latitude wolf spider species.

Keywords: Arctic environment, biometry, altitude, environmental gradients, *Pardosa*, cocoon.

## Introduction

Life history traits are essential to determine the distribution of species and populations. In the Arctic, the relatively harsh environmental conditions can amplify biological phenomena witnessed in temperate regions, allowing us to observe changes in life history traits at smaller geographic scales (Berteaux et al. 2004, Duarte et al. 2012). For example, the same pattern of a given morphological trait might be visible along a shorter spatial gradient in the Arctic than in a temperate region. Because of this, the Arctic has become a major focus of ecological research in the context of climate change (Høye and Sikes 2013). Furthermore, warming is

60   much stronger in the Arctic and at high elevations (Wang et al. 2016), and harsh

61   environmental conditions generally lead to resource limitation (Roff 2002), causing allocation

62   trade-offs: the Arctic is resource-poor compared to temperate regions (Bowden and Buddle

63   2012b; Ameline et al. 2017). Resource limitation is known to drive evolutionary strategies,

64   such as the K, r and A strategies (Greenslade 1983, Holm 1988). Individuals and populations

65   are confronted with multiple environmental constraints along spatial gradients, like latitude or

66   elevation. Abiotic factors such as temperature and growing season length vary across these

67   gradients (Conover and Present 1990), while biotic factors like predation risk also change

68   (Roslin et al. 2017). Changes in elevation also trigger gradients in temperature lapse rate,

69   short-wave radiation input, partial pressure of respiratory gases, precipitation (and related

70   humidity), turbulence and wind speed (Hodkinson 2005, Sundqvist et al. 2013). These

71   changes can occur more abruptly across smaller spatial scales in elevation gradients compared

72   to latitude gradients. Due to the rapid rate at which climate change is affecting northern

73   ecosystems, it is essential to understand how populations respond to such climatic constraints

74   (Ohlberger 2013). By combining latitudinal and elevational gradients, it may be possible to

75   identify the environmental controls of life history trait variations.

76   Body size is a key trait related to the life history of individuals and can influence a broad

77   range of factors from competition for mates to the amount of resources that an individual can

78   allocate to reproduction. Body size variation along spatial gradients has been studied

79   intensively, as body size is 'a continuously varying trait dependent on a variety of factors

80   operating at different stages in an individual's life' (Chown and Gaston 2010). The conditions

81   under which an organism has developed are reflected in its body size. This makes body size a

82   good labile trait for assessing phenotypic plasticity in response to climatic variability. Since

83   the 19th century, many hypotheses were proposed as 'ecological rules' to try to explain

84   observed variations of body size along geographical gradients. The most famous one is

85   Bergmann's rule which proposes that the body size of endotherms increases with latitude (e.g.

86   Atkinson and Sibly 1997; Blackburn et al. 1999; Shelomi 2012). This rule states that a larger

87   organism has a reduced surface to volume ratio, which minimizes heat loss. It has since been

88   extended to include patterns in body size of ectotherms across latitudinal and elevational

89   gradients (Blanckenhorn and Demont 2004; Chown and Gaston 2010; Shelomi 2012, spiders:

90   Entling et al. 2010). Bergmann's rule was set as a temperature effect while the converse

91   Bergmann's rule has been set as a season length effect (Sheridan and Bickford 2011). This

92   extension to the rule supposes that shorter seasons at higher latitudes reduce the foraging

93   period, resulting in a limited growth and development period (Mousseau 1997). A gradient of

94   decreasing body size towards the poles should then be observable (Blanckenhorn and Demont

95   2004). Another rule, the countergradient variation is also linked to seasonal limitations and

96   assumes that populations at higher latitudes would compensate for the reduced season length

97   by growing faster (Conover and Present 1990). It is still a controversial subject and there is no

98   clear explanation as to why body size increases or decreases when an organism is exposed to

99   low temperatures (Angilletta et al. 2004). Studies on ectotherms showed an increased body

100  size of animals reared at lower temperatures, revealing a greater decrease of developmental

101  rate than of growth rate (Forster et al. 2011a, b). This phenomenon is termed the

102  'developmental temperature-size rule' or TSR (Atkinson 1994). There could also be a trade-

103  off between fecundity and a delayed maturity. Delayed maturation leads to a larger body size

104  and an increase in fecundity (Roff 2002).

105  Wolf spiders (Lycosidae) are found in high densities in the Arctic (e.g. Bowden and Buddle

106  2012b). Among this group, female *Pardosa* carry their egg cocoons, or egg sacs, attached to

107  their spinnerets, which allows for specimen-specific measurement of fecundity and quality of

108  the offspring (e.g. Pétillon et al. 2011). Clutch size has previously been considered a proxy for

109  fecundity (e.g. Bowden et al. 2013), as species of *Pardosa* in the Arctic are generally thought

4

110     to produce only one clutch per lifetime and not to overwinter after reproduction (semelparous

111     species, Bowden and Buddle 2012a). Consequently, we expect season length to play a larger

112     role than temperature in the development of these spiders, compared to other species that

113     reproduce multiple times in their lifetime or during multiple seasons. Høye et al. (2009) found

114     in *P. glacialis* that body size varied mostly in relation to season length (timing of snowmelt).

115     Since clutch size is related to body size (Pétillon et al. 2009; Puzin et al. 2011; Hein et al.

116     2015, 2018), we also expect season length to have a greater impact on reproductive traits in

117     *Pardosa* species. Egg volume commonly serves as a proxy for offspring quality, as bigger

118     eggs result in bigger and fitter offspring (Hendrickx and Maelfait 2003).

119     In this study, we measure body size and reproductive traits along elevational gradients at six

120     sites in Arctic and sub-Arctic areas. We aim to determine if closely related species (*Pardosa*

121     spp.) display similar patterns in life history traits along these gradients. We test the following

122     hypotheses: (1) As we expect season length to play a greater role than temperature in

123     development, body size decreases with elevation, following a converse Bergmann's cline

124     (spiders: latitude: Puzin et al. 2014, elevation: Høye and Hammel 2010; Bowden et al. 2013;

125     Hein et al. 2015). This is the case in most terrestrial univoltine arthropods (Horne et al. 2015),

126     and we expect similar constraints on the *Pardosa* species we studied. (2) As resources are

127     more limited in high elevation, clutch size decreases with elevation; provided that female

128     body size also decreases with elevation, as we know that reproductive outputs are linked to

129     body size (Bowden et al. 2013); and egg volume increases with elevation, revealing a

130     quantity/quality trade-off in female fecundity in response to harsh environmental conditions

131     (Hendrickx et al. 2003; Puzin et al. 2011).

132

133

## Material and Methods

### Collected species

We collected four different species belonging to the genus *Pardosa* (Araneae, Lycosidae): *P. hyperborea* (Thorell 1872), *P. palustris* (Linnaeus 1758), *P. glacialis* (Thorell 1872) and *P. furcifera* (Thorell 1875), with contrasted habitat preferences, but most are thought to produce only one clutch per lifetime (semelparous species) (see Table 1 for life cycle information and Online Resource 1 for habitat data). Most Arctic and sub-Arctic *Pardosa* species have multi-year life cycles (at least two years), overwintering as young juveniles in their first winter and as sub-adults in their second winter (Edgar 1971; Pickavance 2001; Høye et al. 2009; Bowden and Buddle 2012b). Growing season spans from May-June to August-September depending on the species, location and sex (Table 1).

We collected *P. hyperborea* at three different sites in Greenland (Kobbefjord, Godthaabsfjord and Narsarsuaq), *P. palustris* in Iceland and in the Faroe islands, *P. glacialis* in Greenland (Zackenberg) and *P. furcifera* in Greenland (Kobbefjord) (Figure 1, Table 2). As we only collected three individuals of *P. furcifera* at high elevation, we did not test the effect of elevation on this species (Table 2). We hand collected over a small period of time (maximum of two weeks, Table 2) at each site. We collected thirty females with egg sacs at each point when possible (Table 2) within a relatively small area ('collection point'; $< 50$ m$^2$) and preserved them in 70% ethanol. We sampled either in 50 meter a.s.l. intervals along an elevational gradient or at low versus high elevations, depending on the elevational distribution of the species (Table 2, Online Resource 2). Lycosidae in boreal and Arctic regions are non-web building species (Marusik 2015). We believe that no migration was possible between collection points as they are separated by several kilometers, except for Kobbefjord (*P. hyperborea*) and Zackenberg (*P. glacialis*), where spiders were collected along a two kilometer regular slope, i.e. every 500 m (Online Resource 2).

159

**Laboratory measurements**

We estimated body size, fecundity and egg quality by prosoma width, clutch size, and mean

egg volume, respectively in the laboratory with a EUROMEX trinocular stereomicroscope

45X, magnification 25X, connected with a CMEX5000 camera. Pictures and measurements

were taken with the software EUROMEX ImageFocus v3.0. For each individual, we

measured the following attributes: tibia length of leg I pair, length and width of the prosoma,

clutch size (number of eggs) and mean length and width of ten randomly subsampled eggs

(see Online Resource 3 for pictures). We calculated mean egg volume using the formula:

$Volume = \frac{\pi}{6} \times length \times width^2$ following Hendrickx and Maelfait (2003). We divided

embryonic stages into six categories: I: only cells are visible; II: legs are visible; III: the

prosoma is developed; IV: the prosoma is hatched and no measurement is possible; V: the

postembryonic individual is hatched within the egg sac; VI: the postembryonic individual has

emerged from the egg sac (Online Resources 3 and 4). We used this last stage when the

collection in ethanol made the postembryonic individuals (1st instar larvae) exit the egg sac.

Since we always collected a female with an intact egg sac, we assume not to have lost any

individuals. A large proportion of the egg sacs (34 % of all individuals) contained eggs, which

had hatched when dissected (stages IV to VI). This bias is however difficult to avoid given

that sampling cannot be done with exact synchrony in the field. Due to the variation in the

development of eggs, we considered mean egg volume as a less reliable trait than clutch size,

and refrained from using a global variable connecting clutch size and mean egg volume. We did

all measurements on all four species, with a total of 775 females. Of the 775 individuals in total,

14 cocoons (13-low, 1-high elevation) of *P. hyperborea* were found to be parasitized from the

Narsarsuaq (South Greenland) site. No parasitism was found in the other three species. This

represented an incidence of 1.8% parasitism for all data combined, but 18% of the population of

7

184 *P. hyperborea* collected from the low site at Narsarsuaq. Teneral adults were identified as *Gelis*

185 *sp.* (Hymenoptera, Ichneumonidae, Cryptinae) (Online Resource 3, Figures 2.1 to 2.3).

186

187 **Analyses**

188 In order to get a representative measurement of body size, correlations were assessed between

189 all of our size measurements. Prosoma width was correlated with prosoma length, left tibia

190 length and right tibia length by 99% (*Pearson correlation test*, $t = 170.0$, $df = 763$, $p <$

191 $0.0001$), 95% ($t = 83.8$, $df = 738$, $p < 0.0001$) and 95% ($t = 84.9$, $df = 732$, $p < 0.0001$),

192 respectively. Hence, we chose to use prosoma width as a proxy of body size (as used in Jakob

193 et al. 1996). Henceforth we refer to prosoma width as body size if not stated otherwise. First,

194 the effects of elevation on body size and on reproductive traits were assessed. Sampling

195 differences (Table 2) necessitated that we tested for the effects of elevation on species and

196 sites, separately. Second, the effect of body size on reproductive traits was assessed for our

197 entire data set and for each species separately. All measurements were normally distributed

198 (Online Resource 5). Linear models were applied, LLSR (Linear Least Squares Regression) in

199 the case of continuous explanatory variables, ANCOVA (Analysis of Covariance) in the case

200 of both continuous and categorical explanatory variables and factors. When testing for the

201 effect of elevation, we included collection point as a random effect to avoid site-specific

202 effects using linear mixed models (function 'lmer' in R package 'lme4', Bates et al. 2015).

203 For testing the effects of elevation on reproductive traits, we always include female body size

204 as a covariate. Significance of explanatory variables and factors was tested via an ANOVA

205 test using type III sums of squares (package 'car': Fox and Weisberg 2011), i.e., without

206 taking the order of the explanatory variables/factors into account. Finally, normal distribution

207 of the residuals of the model was tested through a distribution histogram and a quantile-

208 quantile plot. All models are presented in Tables 3 and 4. All means are presented with

209    standard error (package 'RVAideMemoire': Hervé 2015) and all statistics were conducted

210    using the R environment for statistical computing v. 3.3.2 (R Development Core Team 2016).

211

212    **Results**

213

214    **The effect of elevation on body size and reproductive traits**

215    Mean body size (prosoma width) of *Pardosa hyperborea*, *P. palustris*, *P. glacialis* and *P.*

216    *furcifera* were $1.85 \pm 0.006$ mm ($n = 465$), $2.17 \pm 0.013$ mm ($n = 90$), $2.60 \pm 0.012$ mm ($n =$

217    151) and $3.05 \pm 0.020$ mm ($n = 59$), respectively. Mean body size of *P. hyperborea* was larger

218    in Kobbefjord with mean sizes of $1.95 \pm 0.0096$ mm ($n = 178$), $1.80 \pm 0.0071$ mm ($n = 166$)

219    in Godthaabsfjord and $1.78 \pm 0.0077$ mm ($n = 123$) in Narsarsuaq, (*ANOVA*, $p < 0.0001$,

220    *TukeyHSD test*, $p < 0.0001$). Elevation had no effect on the body size of *P. glacialis* ($p =$

221    0.56) or of *P. hyperborea* in Godthaabsfjord ($p = 0.72$) or Kobbefjord ($p = 0.44$, Table 3,

222    Figure 2a). There was a positive effect of elevation on body size for *P. hyperborea* in

223    Narsarsuaq ($p = 0.049$, Table 3, Figure 2a). At the lower elevation, mean body size was 1.77

224    $\pm 0.009$ mm ($n = 52$) compared to $1.80 \pm 0.013$ mm ($n = 71$) at the higher elevation. Similarly,

225    elevation had a positive effect on *P. palustris* body size ($p = 0.0092$, Table 3, Figure 2a):

226    mean body size was $2.09 \pm 0.019$ mm ($n = 30$) at the lower elevation compared to $2.23 \pm$

227    0.023 mm ($n = 30$) at the higher elevation.

228    Elevation did not have an effect on clutch size for *P. glacialis* ($p = 0.40$), *P. hyperborea* in

229    Godthaabsfjord ($p = 0.19$) and Narsarsuaq ($p = 0.065$) and for *P. palustris* ($p = 0.12$) (Table 3,

230    Figure 2b). For *P. hyperborea* in Kobbefjord, elevation did have a negative effect on clutch

231    size ($p = 0.00039$, Table 3, Figure 2b): clutch size at the lowest elevation was $39 \pm 1$ ($n = 60$)

9

232    compared to $27 \pm 1$ ($n = 30$) at the highest elevation. Elevation did not have any effect on

233    mean egg volume for all species and sites: *P. glacialis* ($p = 0.46$), *P. hyperborea* in

234    Godthaabsfjord ($p = 0.39$), Kobberfjord ($p = 0.73$) nor *P. palustris* ($p = 0.96$) (Table 3, Figure

235    2c). This effect was not tested for *P. hyperborea* in Narsarsuaq as only 5 females carried

236    unhatched eggs.

237    **The effect of body size on reproductive traits**

238    There was an effect of species ($p < 0.0001$), a positive effect of female body size ($p < 0.0001$)

239    and an effect of their interaction on clutch size ($p < 0.0001$) (Table 4), meaning that the effect

240    differed between species. Specifically, the positive effect of female body size on clutch size

241    was stronger for larger species (Figure 3, regression slopes: *P. hyperborea*: $33.04 \pm 2.26$, *P.*

242    *palustris*: $47.53 \pm 7.28$, *P. glacialis*: $82.93 \pm 7.20$, *P. furcifera*: $81.02 \pm 12.77$). There was no

243    effect of species ($p = 0.33$), body size ($p = 0.15$) nor their interaction ($p = 0.44$) on mean egg

244    volume (Table 4), meaning that mean egg volume varied independently from female body

245    size.

246

247    **Discussion**

248

249    **Body size patterns along elevational gradients among sites and species**

250    For *Pardosa palustris* and *P. hyperborea* at one collection site, female body size increased

251    between low and high elevation, however female size in *P. glacialis* and *P. hyperborea* at the

252    two other sites did not respond to elevation. Hence, it appears that body size of *P. palustris*

253    and *P. hyperborea* are more sensitive to elevation than *P. glacialis* and that the smaller

254    species are more sensitive to elevational gradients. This result contradicts our first hypothesis,

which was that spiders would be smaller at higher elevations. Similarly, Hein et al. (2015) did

not find any general body size pattern along elevational gradients. Conversely, Høye and

Hammel (2010) did find a decrease in body size on female *P. glacialis* at high elevation.

Body size patterns along elevation could be species-specific (Høye and Hammel 2010;

Bowden et al. 2013) or may depend on the body size of the species in question (Blanckenhorn

and Demont 2004). Such variation could arise from the combined effect of life-history traits,

habitat, latitude and movement as we discuss below.

We observed different patterns among species that can be triggered by differences in life-

history traits (see Table 1). We know that *P. glacialis* individuals take multiple years to reach

adult size (Høye et al. 2009 and Marusik 2015: Table 1), but smaller species may require less

time to reach adulthood. We assume that the larger species *P. furcifera* also has a longer life-

cycle, although this is not documented. These species could thus increase their development

time to be able to grow larger, trading delayed maturity for a larger body size, in spite of the

possible disadvantages of a longer development time. This suggests that larger Arctic

*Pardosa* species might have developed a distinct strategy to tackle environmental challenges.

Ecological trade-offs have also been described in temperate forest wolf spiders, e.g. risk of

freezing vs. ability to grow at low temperatures (Whitney et al. 2014). However,

phylogeography (Gür 2010), adaptation (Stillwell 2010) or biological interactions (e.g.,

Callaway et al. 2002) might also help explain size responses to elevation.

Temperature is known to decrease approximately 0.5-0.55°C with an increase of 100 m in

elevation (Marshall et al. 2007), while growing season becomes shorter with elevation

(O'Neill et al. 2015). We know that climate change is stronger in the Arctic and at high

elevations (Wang et al. 2016), which causes earlier snowmelt and thus relatively longer

growing seasons (Semmens et al. 2013). It is estimated that a 1°C increase in mean annual

temperature would result in a range change of ~167 m in elevation and ~145 km in latitude

280    (Jump et al. 2009). It has been shown in a large variety of terrestrial arthropods that larger

281    species are less affected by warming than smaller species (Forster et al. 2012). This could

282    allow large *Pardosa* species to become even larger in response to climate change.

283    Intraspecifically, it remains difficult to predict the effects of increasing temperatures along

284    elevational gradients, as elevation-body size clines often appear to deviate from temperature-

285    body size cline measured in the laboratory (Horne et al. 2018).

286    Local habitat variation could also drive the patterns in body size along elevational gradients,

287    as habitats change rapidly over elevational gradients. Indeed, body size trends in similar

288    groups have been shown to be affected by local habitat variation (Høye et al. 2009; Bowden

289    et al. 2015). Previous studies of Arctic spider assemblages have also suggested that habitat is

290    a key determinant in species turnover across elevation in these ecosystems (Bowden and

291    Buddle 2010, wet vs. dry habitats: Ernst et al. 2016; Hansen et al. 2016b; Cameron and

292    Buddle 2017; Høye et al. 2018).

293    In our study, we could not disentangle the effect of species from that of latitude because all

294    species were not present at all sampling sites, and this is why we ran separate models for each

295    species and sites. As a consequence, latitudinal effects could mask or supress elevational

296    effects. We found distinct patterns of body size and reproductive traits along separate

297    elevational gradients in the same species (*P. hyperborea*) sampled at nearby sites (the

298    Kobbefjord population was sampled between 40 km and 100 km away from the

299    Godthaabsfjord populations during the same period in the same year (Table 2), which

300    suggests that latitude is not the primary factor that affects elevational patterns in our study

301    species. We suggest that variation in microhabitat influenced our results, while inter-annual

302    climatic variation could also have played a role. We found our largest species, *P. furcifera*, in

303    South Greenland, although only three individuals were collected at high elevations. Further

304    sampling of this species or other large species such as *P. groenlandica* are necessary to test

305 the hypothesis that larger species are less sensitive to environmental changes, regardless of

306 latitude. We sampled *P. glacialis* in Zackenberg (North-East Greenland), although it is also

307 found at lower latitudes in South-West Greenland but at low abundances and only at high

308 elevations (Hansen et al. 2016a). Adaptation to harsher climatic conditions at higher latitudes

309 could also explain why we do not observe body size nor reproductive traits responses to

310 elevation in *P. glacialis*.

311 Some *Pardosa* species have been shown to be able to actively migrate to maximum distances

312 of 500 m per day (*P. pullata, P. prativaga*, Richter et al. 1971), 50 m in 10 min (*P. lapidicina*,

313 Morse 2002), 280 m per day (*P. monticola* in moss dunes, Bonte et al. 2003), or 40-150 m

314 over several months (*P. pullata, P. chelata,* Hallander 1967). We know that wolf spiders are

315 able to migrate in response to environmental cues (Kraus and Morse 2005), and such shifts to

316 suitable microhabitats may constitute a protective behaviour (Schaefer 1977). Since we do

317 observe a pattern of body size in Kobbefjord in *P. hyperborea*, we suppose that migration

318 does not play a significant role there. *P. glacialis* was collected along an elevational gradient

319 of just 200 meters as well, but we do not observe a pattern of body size, so perhaps this

320 environmental gradient was not sufficient to elicit an effect in this species.

321

322 **Interspecific differences in reproductive traits responses to elevation**

323 We found that clutch size and egg volume varied independently of elevation for *P. glacialis*

324 and *P. palustris* while for *P. hyperborea* in Kobbefjord, clutch size decreased with elevation,

325 but egg volume did not show any pattern. Similarly, Hein et al. (2018) found no variation of

326 the eggs size/number trade-off in *P. palustris* along an elevational gradient. Our results show

327 that *P. hyperborea* responded more strongly to elevation than the other two species. This

328 supports our hypothesis of increased sensitivity of smaller *Pardosa* species to environmental

329 changes, since *P. hyperborea* was the smallest species we collected. The absence of a trend

330    between egg volume and body size can also indicate that the volume or mass of individual

331    eggs is influenced more by a combination of body condition and environmental factors than

332    clutch size (e.g. Bowden and Buddle 2012b). As egg volume does not vary along elevational

333    gradients, it appears unnecessary for the eggs to be larger in colder environments.

334

**Interspecific variation in the relationship between body size and clutch size**

336    For all the species we studied, clutch size increased with body size, while egg volume varied

337    independently of body size. This shows that intraspecifically, larger individuals could

338    increase their fecundity more efficiently than smaller individuals. It has been shown among

339    arthropods that clutch size generally increases with body size (Fox and Czesak 2000),

340    including wolf spiders (Pétillon et al. 2009; Puzin et al. 2011; Hein et al. 2015, 2018). This

341    emphasizes that a larger body size is beneficial for females because it enables them to

342    increase their fecundity and ultimately their fitness.

343    From an interspecific point of view, the larger the species, the higher the rate at which clutch

344    size increases with body size. Hence, larger species could increase their fecundity more

345    efficiently than smaller species. According to the Metabolic Theory of Ecology (MTE),

346    having a larger body size allows one to retain more energy because it is processed slower

347    (Brown et al. 2004). This energy can thus be invested in a higher, albeit usually delayed

348    reproductive output compared to smaller species. Within species, this theory can also explain

349    why larger individuals can invest more in their reproductive output. Here, the reproductive

350    output is associated with clutch size while egg volume is associated with the quality of

351    offspring.

352    Our observation that egg volume was not well predicted by body size in wolf spiders mirrors

353    findings by others (Brown et al. 2003; Hendrickx and Maelfait 2003; Hein et al. 2015).

354    Indeed, investment in individual egg mass or volume does appear to be better explained by

355    body condition than body size in this group (e.g., Bowden and Buddle 2012b).

356

## Conclusion

358    We set out to assess the impact of environmental variation, employed through the use of

359    elevational gradients, on body size and reproductive traits in Arctic wolf spiders. Due to the

360    relative harshness of the environmental conditions in this region, we expected that elevational

361    gradients would serve as local seasonal and temperature gradients. We found that smaller

362    species at the respective sites showed more sensitivity to environmental changes. Second,

363    intra- and interspecifically, larger individuals could increase their fecundity more efficiently

364    than smaller individuals/species. Together, these results suggest that large body size is

365    advantageous in the Arctic environment for these species. Third, it appears that females do

366    not produce larger eggs at higher elevations. This could be explained by the fact that the high

367    variability of alpine microclimatic conditions makes it possible for spiders to find suitable

368    conditions even at higher elevations. Our results also show that there are no large-scale

369    general patterns in species-specific responses to environmental changes, and that micro-

370    climatic conditions along with inter-annual climatic variation probably play a crucial role. We

371    emphasize the need for further studies to measure, along with large-scale gradients, local

372    environmental variables such as soil moisture, temperature, shrub dominance, snow-cover and

373    growing season length.

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384

385  Conflict of Interest: The authors declare that they have no conflict of interest.

386

387

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543

544

545 **Table 1** Life cycle information currently known for the collected species. a: Bowden and Buddle
546 2012a; b: Pickavance 2001; c: Marusik 2015; d: Bowden and Buddle 2010; e: Hammel and Nickel
547 2008; f: Dondale and Redner 1990; g: Buddle 2000; h: inferred from related species in similar latitudes
548 e.g. Edgar 1971; i: Høye et al. 2009; j: Hein et al. 2018. * We propose that *P. furcifera* could have a
549 similar life-span to *P. glacialis*, as they present similar sizes

550

| Species | Life cycle | Development season | Reproduction | Hatching period | Overwintering |
|---|---|---|---|---|---|
| *P. glacialis* | 2-3 years [l] | highest activity: mid-June to late-July at high latitudes [d] males and females: June to August [f] | one clutch per lifetime [a] | egg sacs: July and August [f,i], hatching: August [i] | one or two winters before maturation, females are thought not to overwinter after reproduction [a,b] overwinters in soil cracks and under stones [c] |
| *P. hyperborea* | 2-year life span, inferred from related species [b,g] | males: late May to early August, females: June to September [f] July to (at least) September [b] highest activity: mid-June to late-July at high latitudes [d] | one clutch per lifetime [a] | August to September [b] July [e] egg sacs observed in July and August [f] | one or two winters before maturation, females are thought not to overwinter after reproduction [a,b] |
| *P. furcifera* | 2-3 year life span, inferred from related species [b,g]* | males: mid-June to July, females: mid-June to August [f] highest activity: mid-June to late-July at high latitudes [d] | one clutch per lifetime [a] | egg sacs: July, hatched: mid-August [f] | one or two winters before maturation, females are thought not to overwinter after reproduction [a,b] |
| *P. palustris* | 2-3 year life span, [b,g,h,j] | May and June [f] | 1-3 clutches per lifetime [a,j] | egg sacs: June [f] | one or two winters before maturation, females are thought not to overwinter after reproduction [a,b,h] |

551

552 **Table 2** Sampling details of hand collections of *Pardosa* species. Temperature data was acquired
553 through BioClim (Fick and Hijmans 2017)

| Country | Area | Latitude (DD WGS84) | Longitude (DD WGS84) | Temperature annual range (°C) | Mean temperature of warmest quarter (°C) | Date (dd/mm/yyyy) | Species | Elevation (m a.s.l.) (sampling effort n) |
|---|---|---|---|---|---|---|---|---|
| Greenland | Zackenberg | 74.467 | -20.566 | 32.3 | 2.3 | 05-12/08/2014 | *P. glacialis* | 20m (30)[v], 50m (32), 100m (30)[v], 150m (30), 200m (30)[v] |
| | Kobbefjord | 64.117 | -51.350 | 23.0 | 4.6 | 05-10/07/2013 | *P. hyperborea* <br> *P. furcifera* | 0m (30x2), 50m (30), 100m (30), 150m (30), 200m (30) <br> 0m (30x2)*, 200m (3)* |
| | Godthaabsfjord | 64.144 | -51.474 | 22.8 | 5.1 | 15-29/07/2013 | *P. hyperborea* | 18m (30)[a], 20m (22)[a], 49m (30), 153m (30)*, 402m (23), 678m (30) |
| | Narsarsuaq | 61.183 | -45.371 | 24.8 | 9.0 | 24-31/07/2014 | *P. hyperborea* | 42-54m (71)[v], 400-430m (51)[v] |
| Iceland | Reykjavík | 64.525 | -21.880 | 16.2 | 9.8 | 06/2012 | *P. palustris* | 3-40m (30), 390-410m (30) |
| Faroe Islands | Tórshavn | 62.041 | -6.877 | 12.0 | 8.5 | 12-18/06/2012 | *P. palustris* | 350m (30)* |

554 DD: decimal degrees

555 [a] for models assessing elevation's effects on body size and reproductive traits, 30 individuals were picked randomly from the 18
556 m pool and the 20 m pool.

557 * pools that were not used for models assessing elevation's effects on body size and reproductive traits.

558 [v] pools that were not used for the model assessing elevation's effects on mean egg volume due to variation in development
559 stages.

560

561 **Table 3** Models used to test the effects of elevation on body size and reproductive traits

562

| | | Initial model | Model | Response variable | Explanatory variables | $\beta$ estimate (b) | SE | p |
|---|---|---|---|---|---|---|---|---|
| Effect of elevation on body size | for *Pardosa glacialis* | body size ~ elevation + (1\|site) | *LLSR* | body size | elevation | $2.02 \times 10^{-4}$ | $4.54 \times 10^{-4}$ | 0.56 |
| | for *P. hyperborea* in Godthaabsfjord | body size ~ elevation + (1\|site) | *LLSR* | body size | elevation | $1.53 \times 10^{-5}$ | $5.47 \times 10^{-5}$ | 0.72 |
| | for *P. hyperborea* in Kobbefjord | body size ~ elevation + (1\|site) | *LLSR* | body size | elevation | $2.33 \times 10^{-4}$ | $3.62 \times 10^{-4}$ | 0.44 |
| | for *P. hyperborea* in Narsarsuaq | body size ~ elevation + (1\|site) | *LLSR* | body size | elevation | $9.77 \times 10^{-5}$ | $8.14 \times 10^{-5}$ | **0.049** |
| | for *P. palustris* in Iceland | body size ~ elevation + (1\|site) | *LLSR* | body size | elevation | $3.64 \times 10^{-4}$ | $3.75 \times 10^{-4}$ | **0.0092** |
| Effect of elevation on clutch size | for *P. glacialis* | clutch size ~ body size + elevation + (1\|site) | *ANCOVA* | clutch size | body size | 81.74 | 7.44 | **< 0.0001** |
| | | | | | elevation | 0.016 | 0.025 | 0.40 |
| | for *P. hyperborea* in Godthsaabsfjord | clutch size ~ body size + elevation + (1\|site) | *ANCOVA* | clutch size | body size | 42.05 | 4.13 | **< 0.0001** |
| | | | | | elevation | $3.50 \times 10^{-3}$ | $3.00 \times 10^{-3}$ | 0.19 |
| | for *P. hyperborea* in Kobbefjord | clutch size ~ body size + elevation + (1\|site) | *ANCOVA* | clutch size | body size | 31.33 | 3.11 | **< 0.0001** |
| | | | | | elevation | -0.072 | 0.013 | **0.00039** |
| | for *P. hyperborea* in Narsarsuaq | clutch size ~ body size + elevation + (1\|site) | *ANCOVA* | clutch size | body size | 24.35 | 6.60 | **0.00015** |
| | | | | | elevation | $6.30 \times 10^{-3}$ | $6.86 \times 10^{-3}$ | 0.065 |
| | for *P. palustris* in Iceland | clutch size ~ body size + elevation + (1\|site) | *ANCOVA* | clutch size | body size | 66.72 | 9.39 | **< 0.0001** |
| | | | | | elevation | -0.010 | $9.4 \times 10^{-3}$ | 0.12 |
| Effect of elevation on mean egg volume | for *P. glacialis* | mean egg volume ~ body size + elevation + (1\|site) | *ANCOVA* | mean egg volume | body size | $1.07 \times 10^{-2}$ | $7.41 \times 10^{-2}$ | 0.80 |
| | | | | | elevation | $5.77 \times 10^{-5}$ | $3.99 \times 10^{-4}$ | 0.46 |
| | for *P. hyperborea* in Godthsaabsfjord | mean egg volume ~ body size + elevation + (1\|site) | *ANCOVA* | mean egg volume | body size | $1.25 \times 10^{-2}$ | $4.11 \times 10^{-2}$ | 0.77 |
| | | | | | elevation | $-3.15 \times 10^{-5}$ | $5.01 \times 10^{-5}$ | 0.39 |
| | for *P. hyperborea* in Kobbefjord | mean egg volume ~ body size + elevation + (1\|site) | *ANCOVA* | mean egg volume | body size | $-2.42 \times 10^{-2}$ | $2.50 \times 10^{-2}$ | 0.36 |
| | | | | | elevation | $2.40 \times 10^{-5}$ | $8.26 \times 10^{-5}$ | 0.73 |
| | for *P. palustris* in Iceland | mean egg volume ~ body size + elevation + (1\|site) | *ANCOVA* | mean egg volume | body size | $-2.81 \times 10^{-3}$ | $5.97 \times 10^{-2}$ | 0.98 |
| | | | | | elevation | $2.29 \times 10^{-6}$ | $4.41 \times 10^{-5}$ | 0.96 |

563 Significant values are written in bold, 'site': collection point.

564

565

**Table 4** Models used to test the effects of body size on reproductive traits

567

| | | Initial model | Model | Response variable | $F$ | $D.f.$ | $R^2$ | $p$ | Explanatory variables | $F$ | $p$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Effect of body size on clutch size | for all species | clutch size ~ species*body size | *ANCOVA* | clutch size | 691.6 | 744 | 0.87 | **< 0.0001** | species | 24.89 | **< 0.0001** |
| | | | | | | | | | body size | 98.37 | **< 0.0001** |
| | | | | | | | | | species : body size | 27.81 | **< 0.0001** |
| Effect of body size on mean egg volume | for all species | mean egg volume ~ species*body size | *ANCOVA* | mean egg volume | 75.73 | 447 | 0.54 | **< 0.0001** | species | 1.16 | 0.33 |
| | | | | | | | | | body size | 2.09 | 0.15 |
| | | | | | | | | | species : body size | 0.91 | 0.44 |

568 Significant values are written in bold,

569
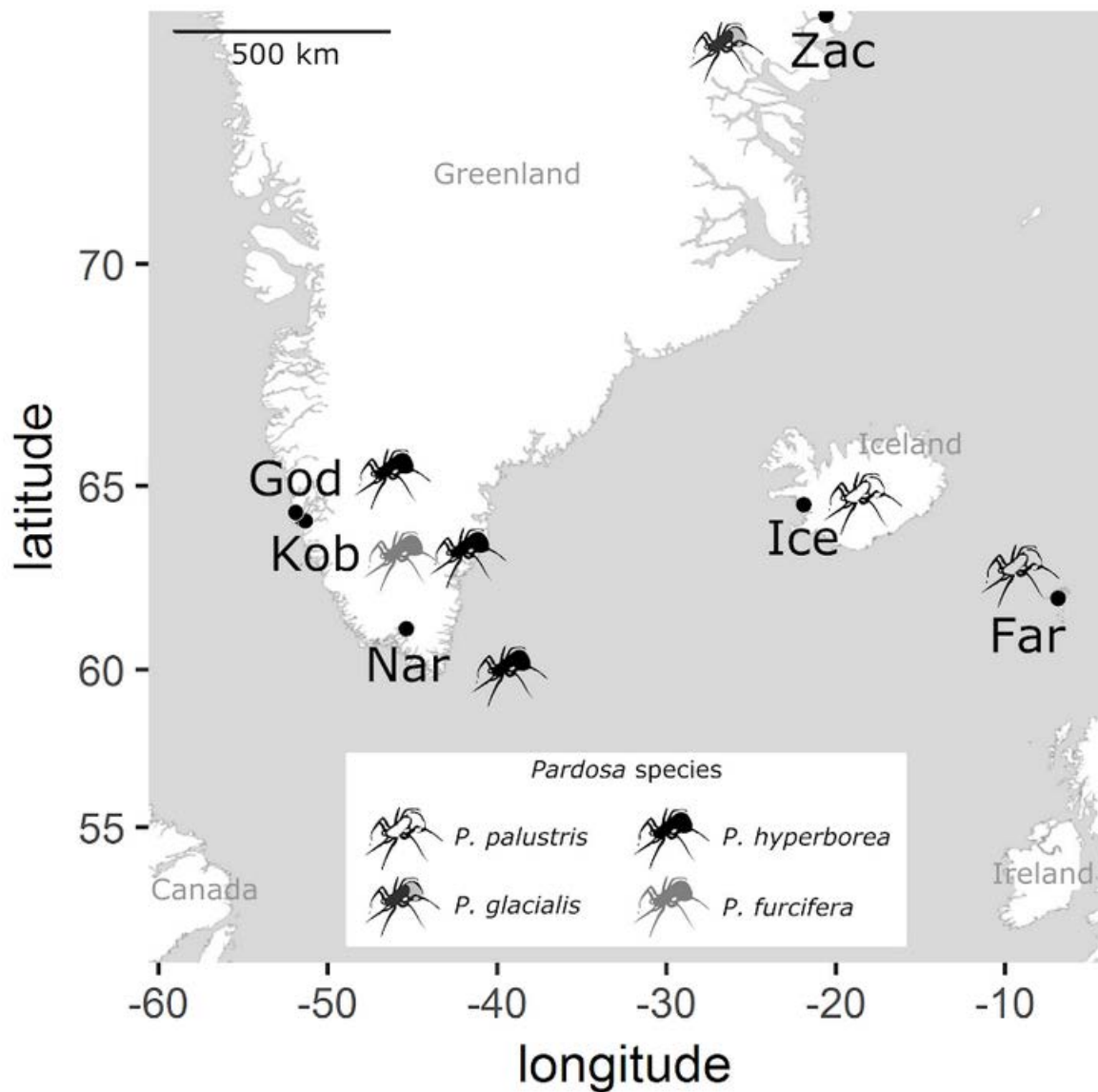
**Fig.1** Map of the collecting sites of *Pardosa* species. From North to South: Zac: Zackenberg (74.467N, 20.566W), Ice: Iceland (64.700N, 21.500W), God: Godthaabsfjord (64.144N, 51.474W), Kob: Kobbefjord (64.117N, 51.350W), Far: Faroe Islands (62.041N, 6.877W), Nar: Narsarsuaq (61.183N, 45.371W). Latitude and longitude in Decimal Degrees WGS84.

574
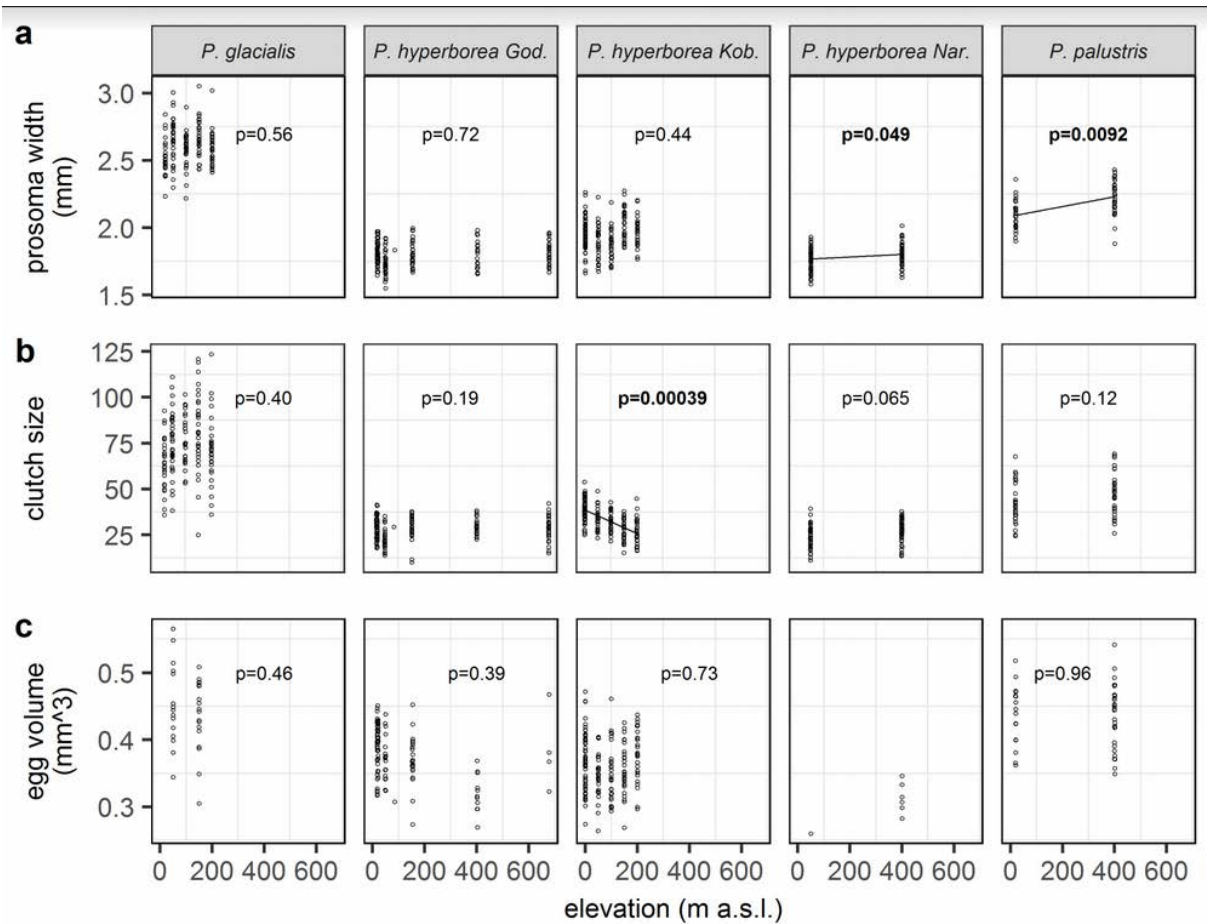
**Fig.2** Effect of elevation on body size, clutch size and mean egg volume. **a.** body size, **b.** clutch size,

**c.** mean egg volume. Sample size was too low for *P. hyperborea* in Narsarsuaq to apply a statistical

test (*n* = 5). Significant values are written in bold. Applied models are detailed in Table 3
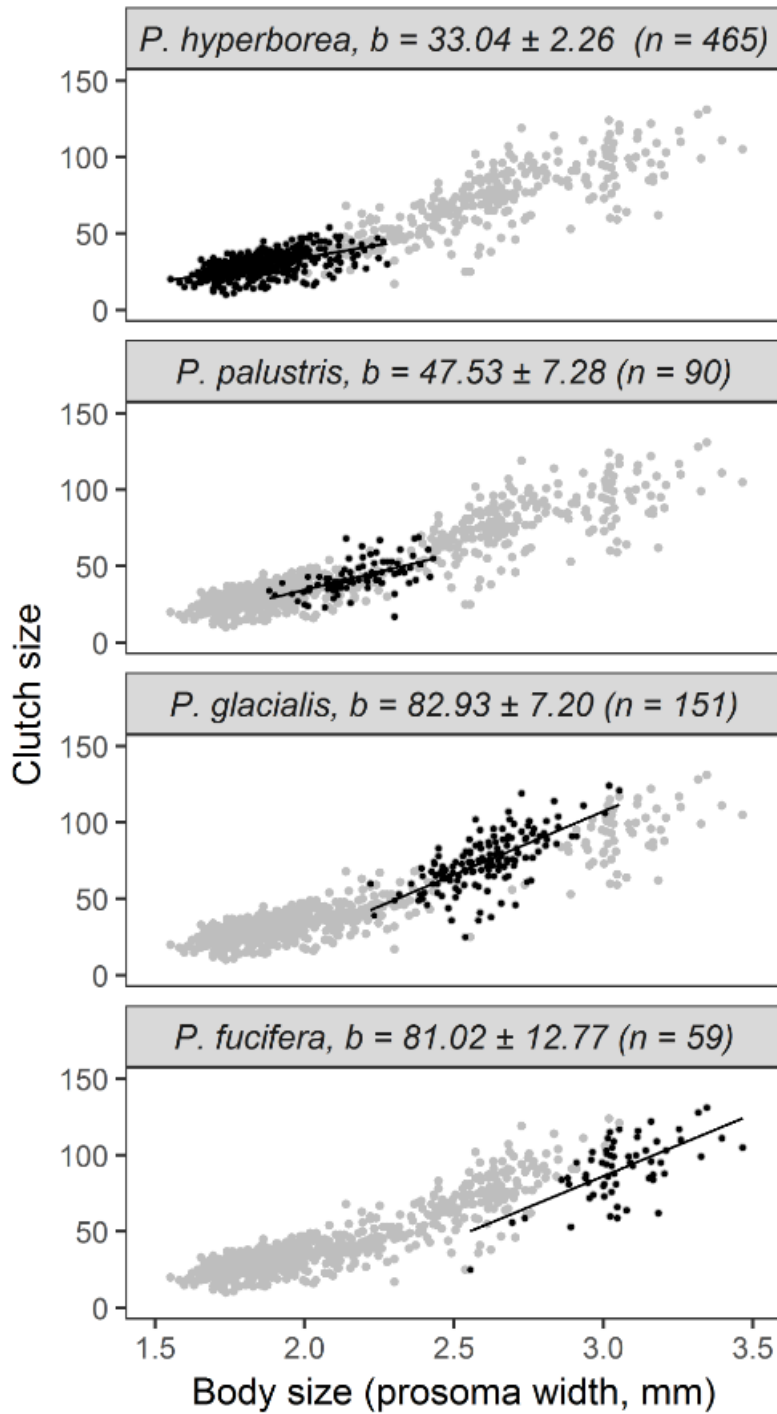
**Fig.3** Linear regression results of clutch size on female size. Formulas are written as follows: $y = a + b * x$. *Pardosa hyperborea*: LLSR, clutch = -31.68 + 33.04*size, $F_{445} = 212.7$, $R^2 = 0.32$, $p < 0.0001$, *P. palustris*: LSSR, clutch = -60.52 + 47.53*size, $F_{88} = 42.67$, $R^2 = 0.32$, $p < 0.0001$, *P. glacialis*: LLSR, clutch = -141.42 + 82.93*size, $F_{149} = 132.7$, $R^2 = 0.47$, $p < 0.0001$, *P. furcifera*: LLSR, Clutch = -159.28 + 81.02*prosoma width, $F_{57} = 30.49$, $R^2 = 0.34$, $p < 0.0001$

Elevational variation of body size and reproductive traits in high latitude wolf spiders (Araneae: Lycosidae)

Polar Biology

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**Online Resource 1** Description of the four species collected on the field. References: 1: Vlijm 1971, 2: Bengtson et al. 1976, 3: Ashmole and Planterose 1979, 4: Bengtson and Hauge 1979, 5: Koponen 1987, 6: Dondale and Redner 1990, 7: Buchar 1993 , 8: Koponen 2002, 9: Cameron et al. 2004, 10: Marusik et al. 2006, 11: Fet and Popov 2007, 12: Hammel and Nickel 2008, 13: Høye and Hammel 2010, 14: Bowden and Buddle 2010, 15: Koponen 2011, 16: Růžička et al. 2012, 17: Hein et al. 2015, 18: Hein et al. 2014, 19: Nentwig et al. 2015, 20: Natural History Museum Bern 2015, 21: Marusik 2015, 22: Hansen et al. 2016

| Species | Description | Distribution | Habitat specialisation | Elevation (m a.s.l.) |
|---|---|---|---|---|
| *P. glacialis* | Thorell 1872 | Holarctic [20], Nearctic, Arctic, Greenland (G) [21] | not specified | 0-860 [13,14,15] |
| *P. hyperborea* | Thorell 1872 | Holarctic [20], low Arctic-boreal [21], Greenland (S, SW north to Disko, SE north to 70°50'N) [21] | rare psychrophilous [7] | 100-1360 [3,5,12,13,14,15,18] |
| *P. furcifera* | Thorell 1875 | Canada, Alaska, Greenland (S, SW [21]), Iceland [20]: trans-Nearctic arcto-alpine range [10, 21] | not specified | 0-1360 [13,14,15] |
| *P. palustris* | Linnaeus 1758 | Holarctic [20] | generalist [7] (widespread, especially in cold climates) [1] | up to 2500 [2,7,9,11] |

| Species | Found habitats |
|---|---|
| *P. glacialis* | in heaths [21] and sedge meadows, among lichens and low shrubs, and on beaches or bare soil on Arctic tundra [6], transition boreal forest to Arctic tundra [14], sub-Arctic pine forest area, birch woods, bogs [21] and treeless fells [15] |
| *P. hyperborea* | open forests and moors [19], birch wood [2,15], sphagnum bogs (in boreal zones [8]), low-lying spruce forests, rocky hillsides, among lichens in Arctic and alpine tundra and on needle mats in forests ofjack pine, black spruce, and balsam fir [6], transition boreal forest to Arctic tundra [14], sub-Arctic pine forest area, birch woods, bogs and treeless fells [15], south-facing dry slopes [21], heath habitats [22] |
| *P. furcifera* | spruce-pine forests, in willow clumps near the timberline, and on moss and stones in alpine tundra [6], sub-Arctic pine forest area, birch woods, bogs and treeless fells [15], transition boreal forest to Arctic tundra [14], on rather moist ground and in *Salix herbacea* snow beds as well as in the moss layer of heaths adjoining brooks. Also in herb fields on slopes and in *Salix glauca* thickets [21] |
| *P. palustris* | open, dry areas [19,17,1], tidal drifts on a saltwater beach, along grassy margins of streams, above timberline in mountain passes [6], rich grassland, poor grassland, ash woodland [9], tundra, mire [16,18], tall herb meadow, grass meadow, birch wood (open ground and sparse woods) [1,2,3], pastures, heaths [1], bogs [8], braided rivers [3], grass and dwarf shrub heaths and open infield meadows [4] |

G: global, S: south, W: west, N: north, E: east

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Elevational variation of body size and reproductive traits in high latitude wolf spiders (Araneae: Lycosidae)
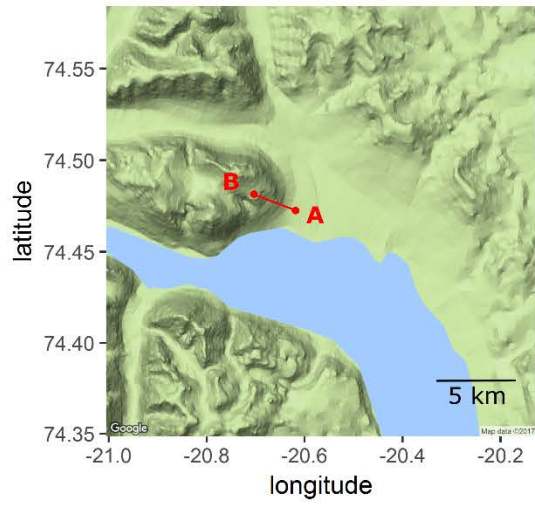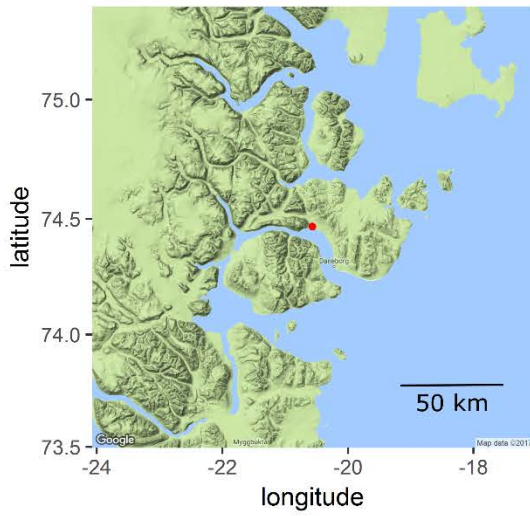
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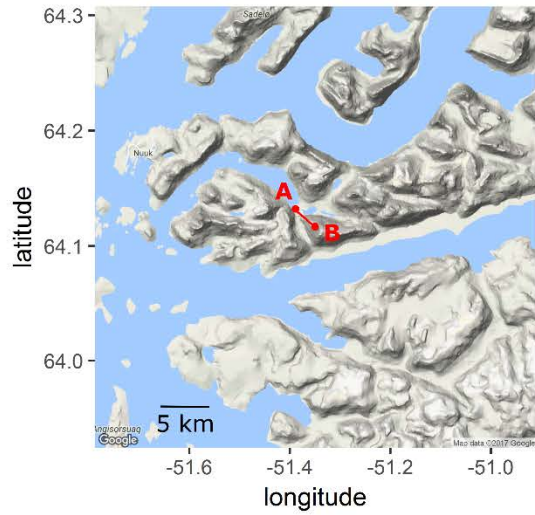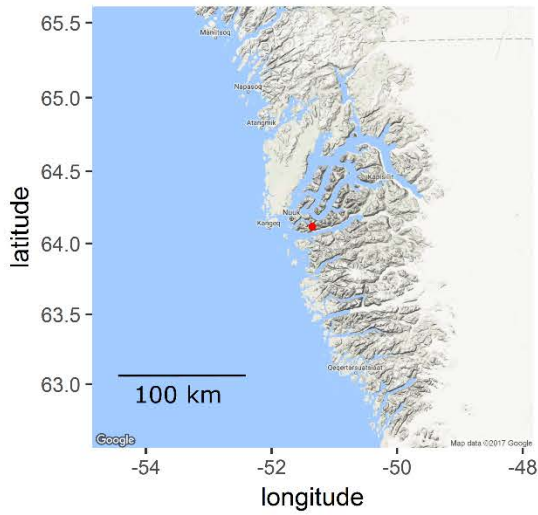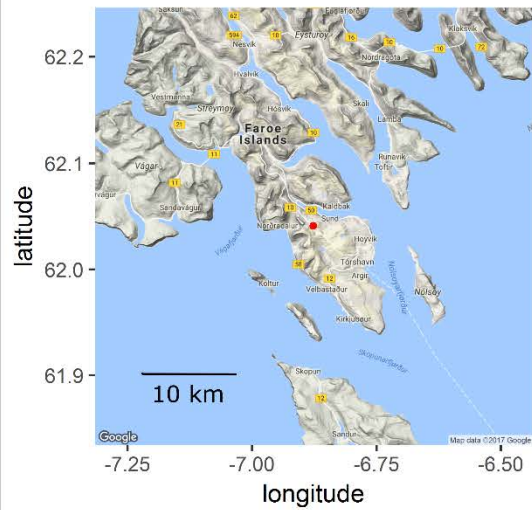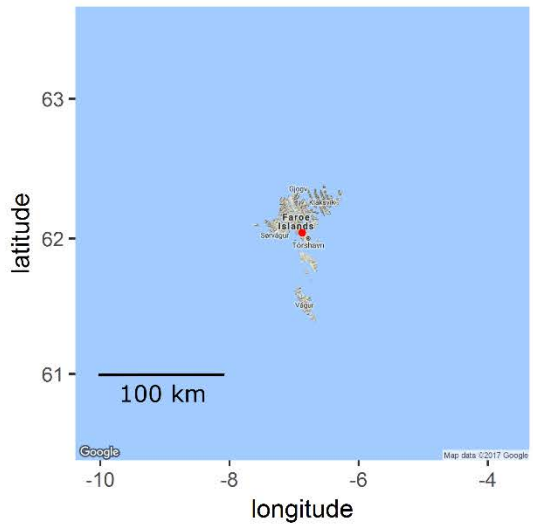
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**Online Resouce 2** Detailed maps of sampling sites. Dots represent collection sites. In Zackenberg and Kobbefjord, 2 km elevation gradients are represented with a segment. *Zackenberg*: A-B: 20-200 m a.s.l.; *Kobbefjord*: 0-200 m a.s.l; *Godthaabsfjord*: A: 18 m a.s.l., B: 20 m a.s.l., C: 50, 150 and 400 m a.s.l., D: 678 m. a.s.l.; *Narsarsuaq*: A: 40-50 m a.s.l., B: 400-430 m a.s.l.; *Iceland*: A: 20 m a.s.l., B: 400 m a.s.l.; *Faroe Islands*: 350 m a.s.l.

Zackenberg

Kobbefjord

Godthaabsfjord
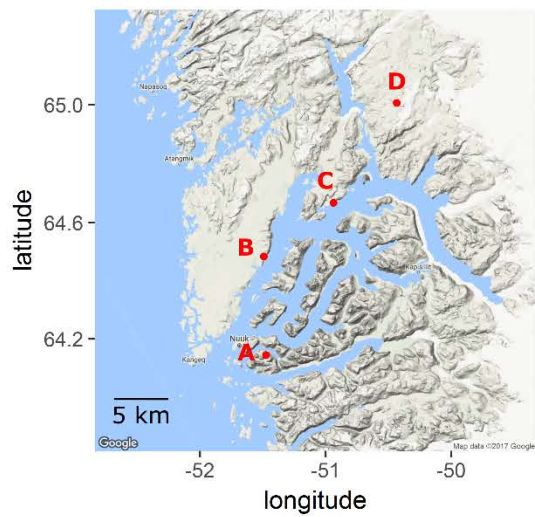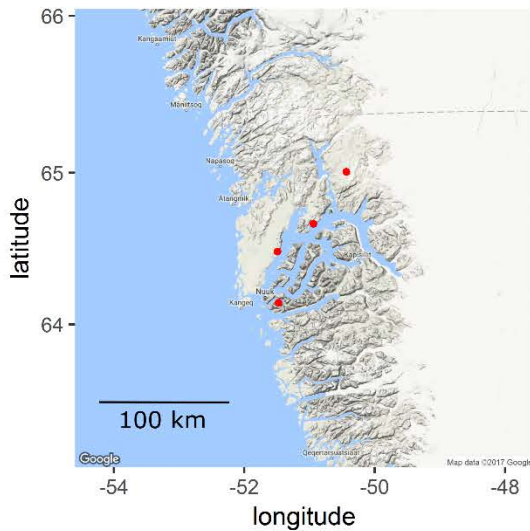
Narsarsuaq
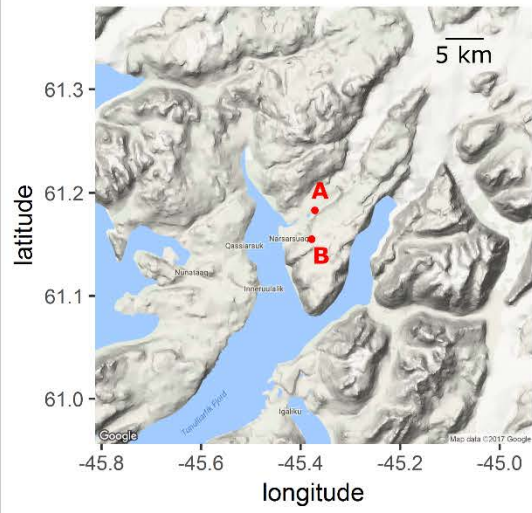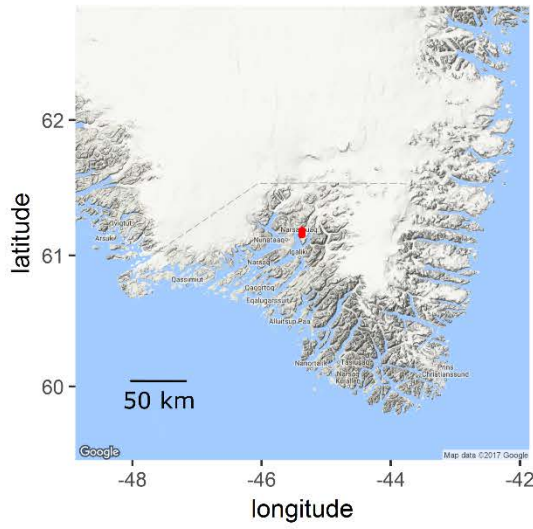
Iceland
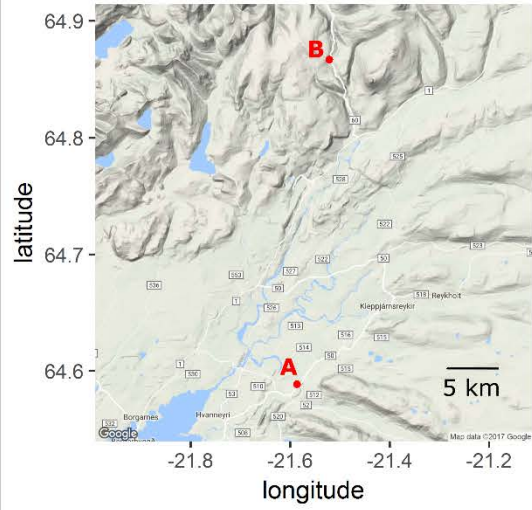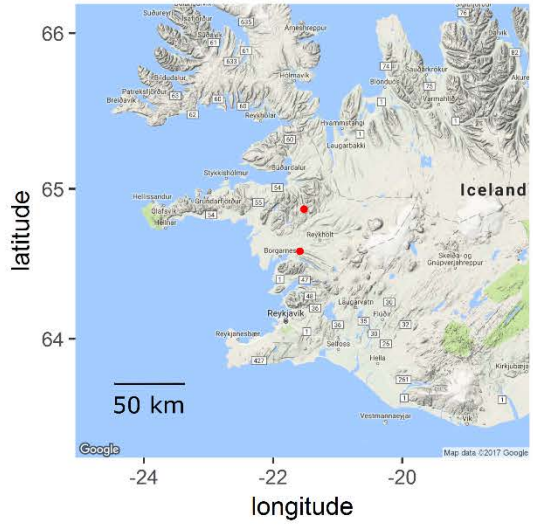
Faroe Islands

Elevational variation of body size and reproductive traits in high latitude wolf spiders (Araneae: Lycosidae)

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**Online Resource 3** Fig.1.1 to 1.6: body measurements and species' prosomas. Fig.2.1 to 2.3: parasitoid developmental stages. Fig.3.1 to 3.12: eggs developmental stages. Arrows represent the measurements. We used a EUROMEX trinocular stereomicroscope 45X connected with a CMEX5000 camera. Pictures and measurements were taken with the software Euromex ImageFocus v3.0.

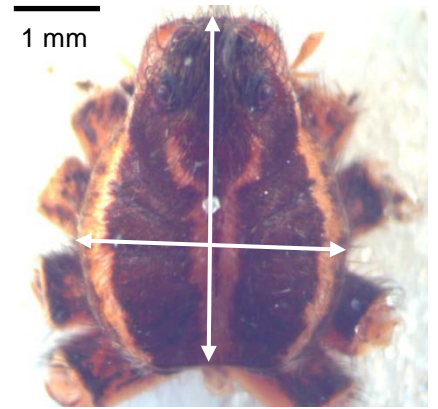**Fig.1.1** *Pardosa palustris* carrying egg sac
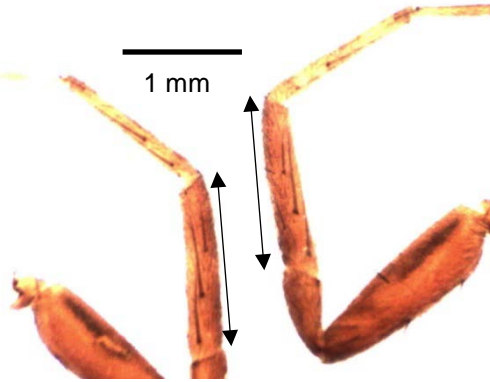


**Fig.1.2** Leg 1's tibias measurement



**Fig.1.3** *P. furcifera*'s prosoma
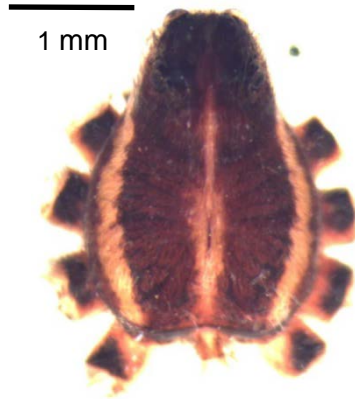


**Fig.1.4** *P. glacialis*' prosoma



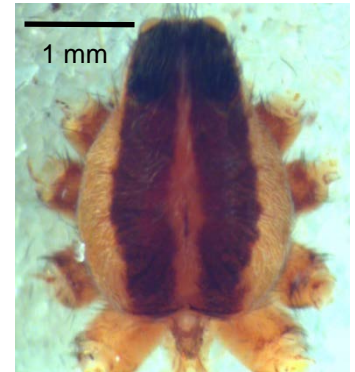**Fig.1.5** *P. palustris*' prosoma



**Fig.1.6** *P. hyperborea*'s prosoma



**Fig.2.1** Parasitoid larvae in egg sac



**Fig.2.2** Parasitoid pupae in egg sac



**Fig.2.3** Parasitoid teneral adults of *Gelis sp.*. Left: wingless ♀, right: ♂ with wings not entirely developed
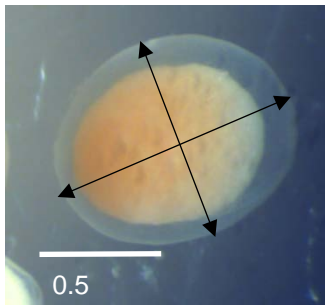
2

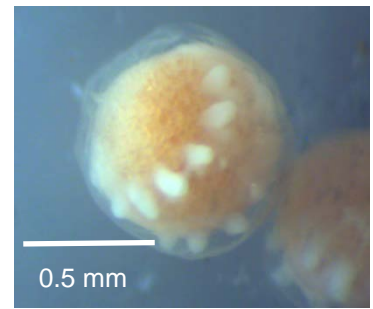**Fig.3.1** Egg development stage I
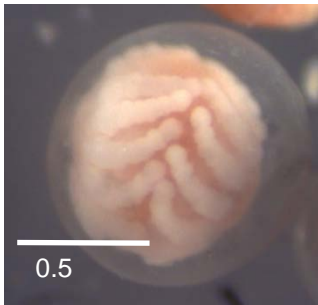


**Fig.3.2** Stage I
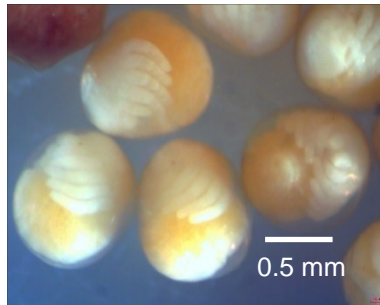


**Fig.3.3** Stage II



**Fig.3.4** Stage II



**Fig.3.5** Stage III
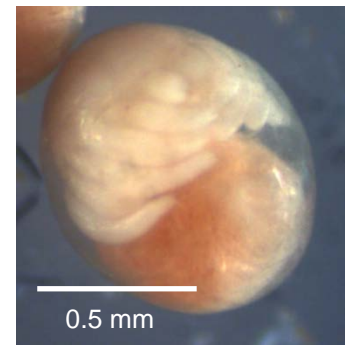


**Fig.3.6** Stage III



**Fig.3.7** Stage IV



**Fig.3.8** Stage V
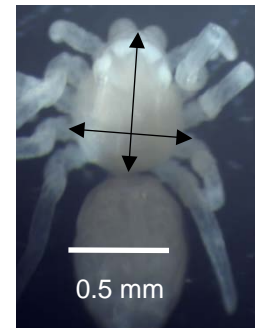


**Fig.3.9** Stage V



**Fig.3.10** Stage V



**Fig.3.11** Stage VI



**Fig.3.12** Stage VI

3

Elevational variation of body size and reproductive traits in high latitude wolf spiders (Araneae: Lycosidae)

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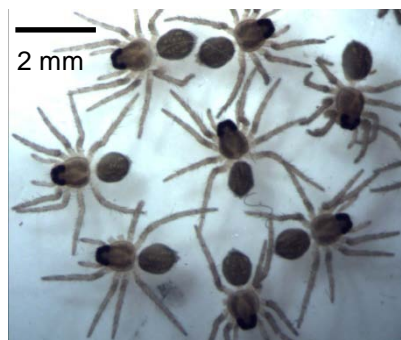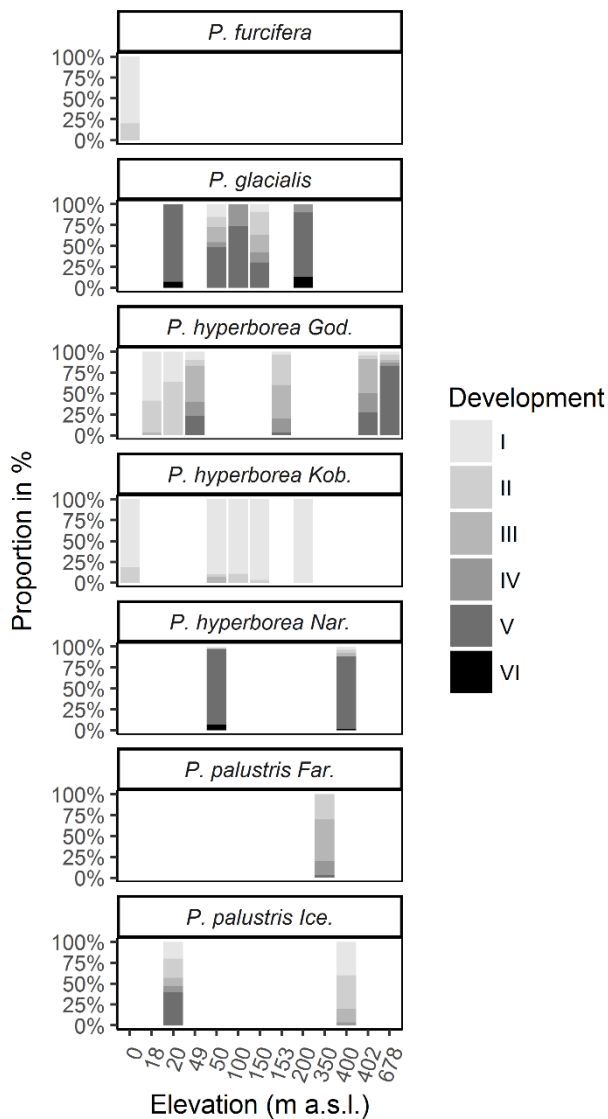**Online Resource 4** Fig. 1: Development stages of eggs in egg sac along elevational gradient per species and site. Development stages: I - VI (see methods). Mean egg volume could only be measured for stages I to III.
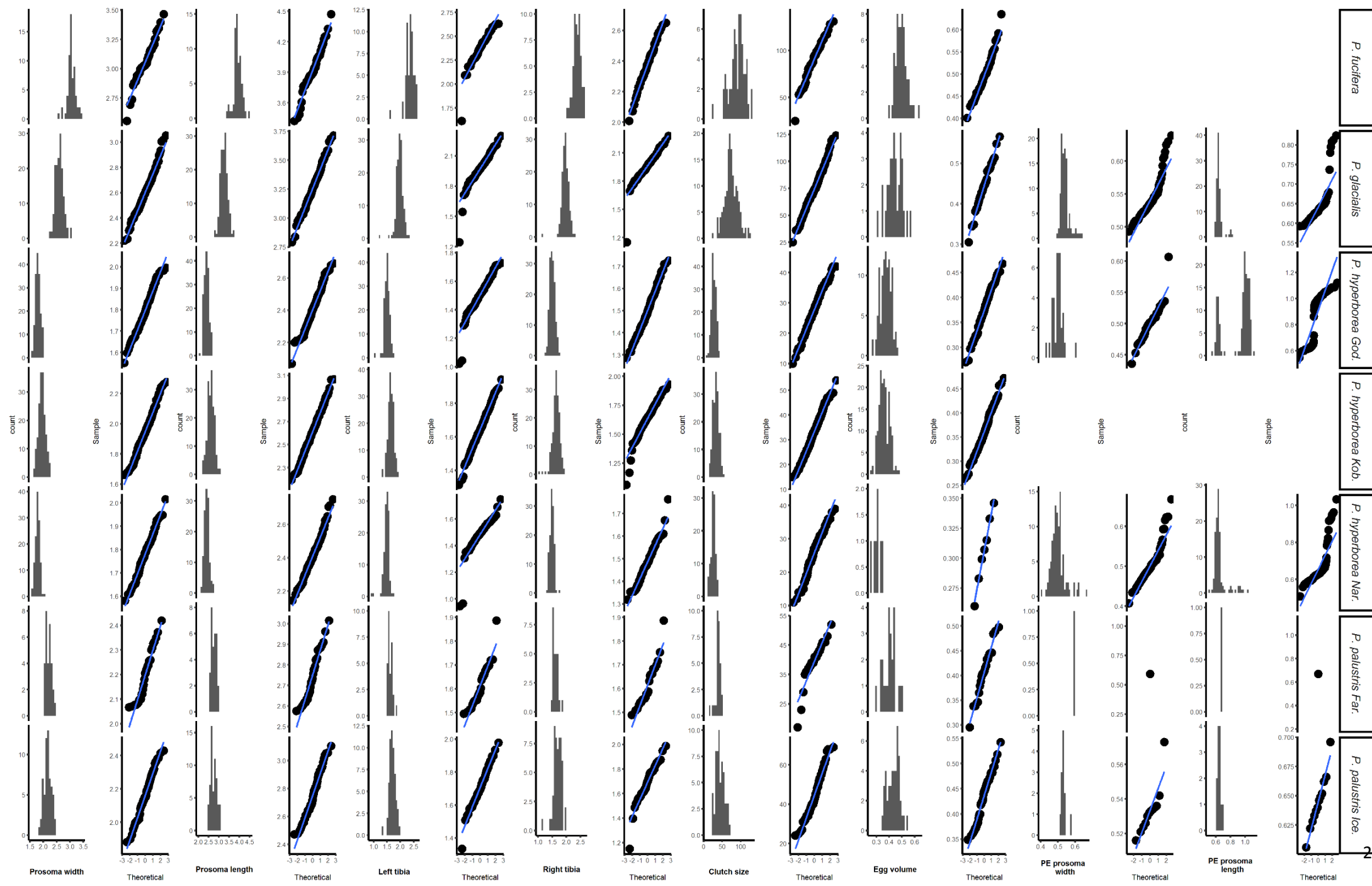
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**Online Resource 5** Fig. 1: Normal distribution of the measured variables. Histograms show the distribution of the measured variable. Corresponding panels on the right show Quantile-Quantile plots (x-axis: Theoretical quantiles, y-axis: Sample quantiles). They were no hatched eggs in female *P. glacialis* and *P. hyperborea* in Kobbefjord. Two distinct distributions in the postembryonic measurements correspond to development stages V and VI. God: Godthaabsfjord, Kob: Kobbefjord, Nar: Narsarsuaq, Far: Faroe Islands, Ice: Iceland. PE: postembryonic.

| | | | | | | | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | | | | | | | | *P. fucifera* |
| | | | | | | | | | | | | | | | | | | | | *P. glacialis* |
| | | | | | | | | | | | | | | | | | | | | *P. hyperborea God.* |
| | | | | | | | | | | | | | | | | | | | | *P. hyperborea Kob.* |
| | | | | | | | | | | | | | | | | | | | | *P. hyperborea Nar.* |
| | | | | | | | | | | | | | | | | | | | | *P. palustris Far.* |
| | | | | | | | | | | | | | | | | | | | | *P. palustris Ice.* |

Prosoma width — Theoretical — Prosoma length — Theoretical — Left tibia — Theoretical — Right tibia — Theoretical — Clutch size — Theoretical — Egg volume — Theoretical — PE prosoma width — Theoretical — PE prosoma length — Theoretical

2