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

3

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36 **Abstract**

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

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

51

52 **Introduction**

53 Life history traits are essential to determine the distribution of species and populations. In the
54 Arctic, the relatively harsh environmental conditions can amplify biological phenomena
55 witnessed in temperate regions, allowing us to observe changes in life history traits at smaller
56 geographic scales (Berteaux et al. 2004, Duarte et al. 2012). For example, the same pattern of
57 a given morphological trait might be visible along a shorter spatial gradient in the Arctic than
58 in a temperate region. Because of this, the Arctic has become a major focus of ecological
59 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. Pétilion 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

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

134 **Material and Methods**

135 **Collected species**

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

145 We collected *P. hyperborea* at three different sites in Greenland (Kobbefjord, Godthaabsfjord
146 and Narsarsuaq), *P. palustris* in Iceland and in the Faroe islands, *P. glacialis* in Greenland
147 (Zackenbergl) and *P. furcifera* in Greenland (Kobbefjord) (Figure 1, Table 2). As we only
148 collected three individuals of *P. furcifera* at high elevation, we did not test the effect of
149 elevation on this species (Table 2). We hand collected over a small period of time (maximum
150 of two weeks, Table 2) at each site. We collected thirty females with egg sacs at each point
151 when possible (Table 2) within a relatively small area ('collection point'; < 50 m²) and
152 preserved them in 70% ethanol. We sampled either in 50 meter a.s.l. intervals along an
153 elevational gradient or at low versus high elevations, depending on the elevational distribution
154 of the species (Table 2, Online Resource 2). Lycosidae in boreal and Arctic regions are non-
155 web building species (Marusik 2015). We believe that no migration was possible between
156 collection points as they are separated by several kilometers, except for Kobbefjord (*P.*
157 *hyperborea*) and Zackenberg (*P. glacialis*), where spiders were collected along a two
158 kilometer regular slope, i.e. every 500 m (Online Resource 2).

159

160 **Laboratory measurements**

161 We estimated body size, fecundity and egg quality by prosoma width, clutch size, and mean
162 egg volume, respectively in the laboratory with a EUROMEX trinocular stereomicroscope
163 45X, magnification 25X, connected with a CMEX5000 camera. Pictures and measurements
164 were taken with the software EUROMEX ImageFocus v3.0. For each individual, we
165 measured the following attributes: tibia length of leg I pair, length and width of the prosoma,
166 clutch size (number of eggs) and mean length and width of ten randomly subsampled eggs
167 (see Online Resource 3 for pictures). We calculated mean egg volume using the formula:
168 $Volume = \frac{\pi}{6} \times length \times width^2$ following Hendrickx and Maelfait (2003). We divided
169 embryonic stages into six categories: I: only cells are visible; II: legs are visible; III: the
170 prosoma is developed; IV: the prosoma is hatched and no measurement is possible; V: the
171 postembryonic individual is hatched within the egg sac; VI: the postembryonic individual has
172 emerged from the egg sac (Online Resources 3 and 4). We used this last stage when the
173 collection in ethanol made the postembryonic individuals (1st instar larvae) exit the egg sac.
174 Since we always collected a female with an intact egg sac, we assume not to have lost any
175 individuals. A large proportion of the egg sacs (34 % of all individuals) contained eggs, which
176 had hatched when dissected (stages IV to VI). This bias is however difficult to avoid given
177 that sampling cannot be done with exact synchrony in the field. Due to the variation in the
178 development of eggs, we considered mean egg volume as a less reliable trait than clutch size,
179 and refrained from using a global variable connecting clutch size and mean egg volume. We did
180 all measurements on all four species, with a total of 775 females. Of the 775 individuals in total,
181 14 cocoons (13-low, 1-high elevation) of *P. hyperborea* were found to be parasitized from the
182 Narsarsuaq (South Greenland) site. No parasitism was found in the other three species. This
183 represented an incidence of 1.8% parasitism for all data combined, but 18% of the population of

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 ± 0.006 mm ($n = 465$), 2.17 ± 0.013 mm ($n = 90$), 2.60 ± 0.012 mm ($n =$
217 151) and 3.05 ± 0.020 mm ($n = 59$), respectively. Mean body size of *P. hyperborea* was larger
218 in Kobbefjord with mean sizes of 1.95 ± 0.0096 mm ($n = 178$), 1.80 ± 0.0071 mm ($n = 166$)
219 in Godthaabsfjord and 1.78 ± 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 ± 0.009 mm ($n = 52$) compared to 1.80 ± 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 ± 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 ± 1 ($n = 60$)

232 compared to 27 ± 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 ± 2.26 , *P.*
242 *palustris*: 47.53 ± 7.28 , *P. glacialis*: 82.93 ± 7.20 , *P. furcifera*: 81.02 ± 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,

255 which was that spiders would be smaller at higher elevations. Similarly, Hein et al. (2015) did
256 not find any general body size pattern along elevational gradients. Conversely, Høye and
257 Hammel (2010) did find a decrease in body size on female *P. glacialis* at high elevation.
258 Body size patterns along elevation could be species-specific (Høye and Hammel 2010;
259 Bowden et al. 2013) or may depend on the body size of the species in question (Blanckenhorn
260 and Demont 2004). Such variation could arise from the combined effect of life-history traits,
261 habitat, latitude and movement as we discuss below.

262 We observed different patterns among species that can be triggered by differences in life-
263 history traits (see Table 1). We know that *P. glacialis* individuals take multiple years to reach
264 adult size (Høye et al. 2009 and Marusik 2015: Table 1), but smaller species may require less
265 time to reach adulthood. We assume that the larger species *P. furcifera* also has a longer life-
266 cycle, although this is not documented. These species could thus increase their development
267 time to be able to grow larger, trading delayed maturity for a larger body size, in spite of the
268 possible disadvantages of a longer development time. This suggests that larger Arctic
269 *Pardosa* species might have developed a distinct strategy to tackle environmental challenges.
270 Ecological trade-offs have also been described in temperate forest wolf spiders, e.g. risk of
271 freezing vs. ability to grow at low temperatures (Whitney et al. 2014). However,
272 phylogeography (Gür 2010), adaptation (Stillwell 2010) or biological interactions (e.g.,
273 Callaway et al. 2002) might also help explain size responses to elevation.

274 Temperature is known to decrease approximately 0.5-0.55°C with an increase of 100 m in
275 elevation (Marshall et al. 2007), while growing season becomes shorter with elevation
276 (O'Neill et al. 2015). We know that climate change is stronger in the Arctic and at high
277 elevations (Wang et al. 2016), which causes earlier snowmelt and thus relatively longer
278 growing seasons (Semmens et al. 2013). It is estimated that a 1°C increase in mean annual
279 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 Intrinspecifically, 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 suppress 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

335 **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

357 **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.

374

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384

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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
<i>P. glacialis</i>	2-3 years ^[f]	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 ^[f]	one or two winters before maturation, females are thought not to overwinter after reproduction ^[a,b] overwinters in soil cracks and under stones ^[c]
<i>P. hyperborea</i>	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]
<i>P. furcifera</i>	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]
<i>P. palustris</i>	2-3 year life span, ^[b,g,h,j]	highest activity: mid-June to late-July at high latitudes ^[d] May and June ^[f]	1-3 clutches per lifetime ^[a,i]	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	Zackenbergl	74.467	-20.566	32.3	2.3	05-12/08/2014	<i>P. glacialis</i>	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	<i>P. hyperborea</i> <i>P. furcifera</i>	0m (30x2), 50m (30), 100m (30), 150m (30), 200m (30) 0m (30x2)*, 200m (3)*
	Godthaabsfjord	64.144	-51.474	22.8	5.1	15-29/07/2013	<i>P. hyperborea</i>	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	<i>P. hyperborea</i>	42-54m (71) ^v , 400-430m (51) ^v
Iceland	Reykjavik	64.525	-21.880	16.2	9.8	06/2012	<i>P. palustris</i>	3-40m (30), 390-410m (30)
Faroe Islands	Tórshavn	62.041	-6.877	12.0	8.5	12-18/06/2012	<i>P. palustris</i>	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	β estimate (b)	SE	p	
Effect of elevation on body size	for <i>Pardosa glacialis</i>	body size ~ elevation + (1 site)	<i>LLSR</i>	body size	elevation	2.02×10^{-4}	4.54×10^{-4}	0.56
	for <i>P. hyperborea</i> in Godthaabsfjord	body size ~ elevation + (1 site)	<i>LLSR</i>	body size	elevation	1.53×10^{-5}	5.47×10^{-5}	0.72
	for <i>P. hyperborea</i> in Kobbe fjord	body size ~ elevation + (1 site)	<i>LLSR</i>	body size	elevation	2.33×10^{-4}	3.62×10^{-4}	0.44
	for <i>P. hyperborea</i> in Narsarsuaq	body size ~ elevation + (1 site)	<i>LLSR</i>	body size	elevation	9.77×10^{-5}	8.14×10^{-5}	0.049
	for <i>P. palustris</i> in Iceland	body size ~ elevation + (1 site)	<i>LLSR</i>	body size	elevation	3.64×10^{-4}	3.75×10^{-4}	0.0092
Effect of elevation on clutch size	for <i>P. glacialis</i>	clutch size ~ body size + elevation + (1 site)	<i>ANCOVA</i>	clutch size	body size	81.74	7.44	< 0.0001
					elevation	0.016	0.025	0.40
	for <i>P. hyperborea</i> in Godthaabsfjord	clutch size ~ body size + elevation + (1 site)	<i>ANCOVA</i>	clutch size	body size	42.05	4.13	< 0.0001
					elevation	3.50×10^{-3}	3.00×10^{-3}	0.19
	for <i>P. hyperborea</i> in Kobbe fjord	clutch size ~ body size + elevation + (1 site)	<i>ANCOVA</i>	clutch size	body size	31.33	3.11	< 0.0001
					elevation	-0.072	0.013	0.00039
	for <i>P. hyperborea</i> in Narsarsuaq	clutch size ~ body size + elevation + (1 site)	<i>ANCOVA</i>	clutch size	body size	24.35	6.60	0.00015
					elevation	6.30×10^{-3}	6.86×10^{-3}	0.065
	for <i>P. palustris</i> in Iceland	clutch size ~ body size + elevation + (1 site)	<i>ANCOVA</i>	clutch size	body size	66.72	9.39	< 0.0001
					elevation	-0.010	9.4×10^{-3}	0.12
Effect of elevation on mean egg volume	for <i>P. glacialis</i>	mean egg volume ~ body size + elevation + (1 site)	<i>ANCOVA</i>	mean egg volume	body size	1.07×10^{-2}	7.41×10^{-2}	0.80
					elevation	5.77×10^{-5}	3.99×10^{-4}	0.46
	for <i>P. hyperborea</i> in Godthaabsfjord	mean egg volume ~ body size + elevation + (1 site)	<i>ANCOVA</i>	mean egg volume	body size	1.25×10^{-2}	4.11×10^{-2}	0.77
					elevation	-3.15×10^{-5}	5.01×10^{-5}	0.39
	for <i>P. hyperborea</i> in Kobbe fjord	mean egg volume ~ body size + elevation + (1 site)	<i>ANCOVA</i>	mean egg volume	body size	-2.42×10^{-2}	2.50×10^{-2}	0.36
					elevation	2.40×10^{-5}	8.26×10^{-5}	0.73
	for <i>P. palustris</i> in Iceland	mean egg volume ~ body size + elevation + (1 site)	<i>ANCOVA</i>	mean egg volume	body size	-2.81×10^{-3}	5.97×10^{-2}	0.98
					elevation	2.29×10^{-6}	4.41×10^{-5}	0.96

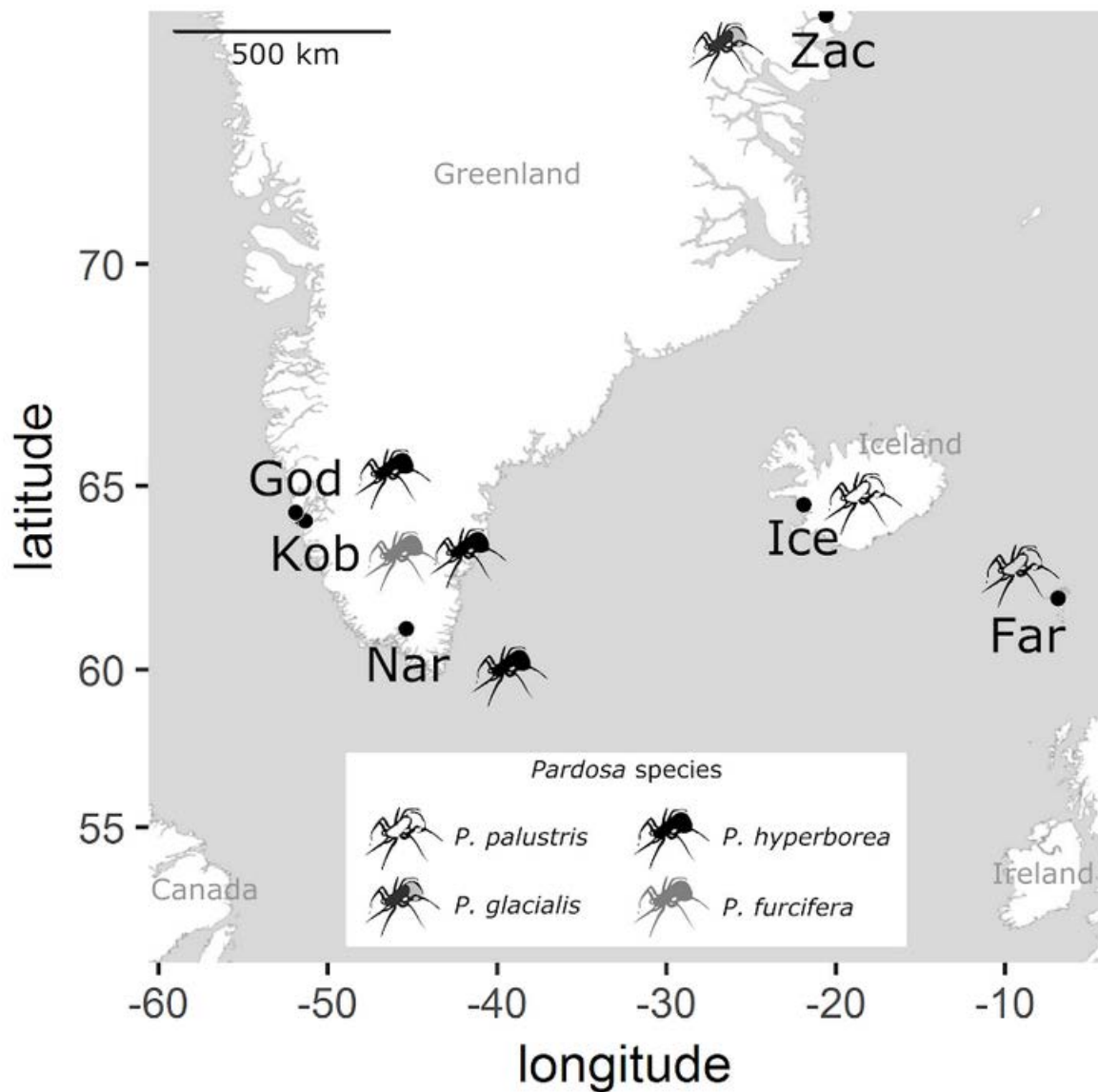
563 Significant values are written in bold, 'site': collection point.

564

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

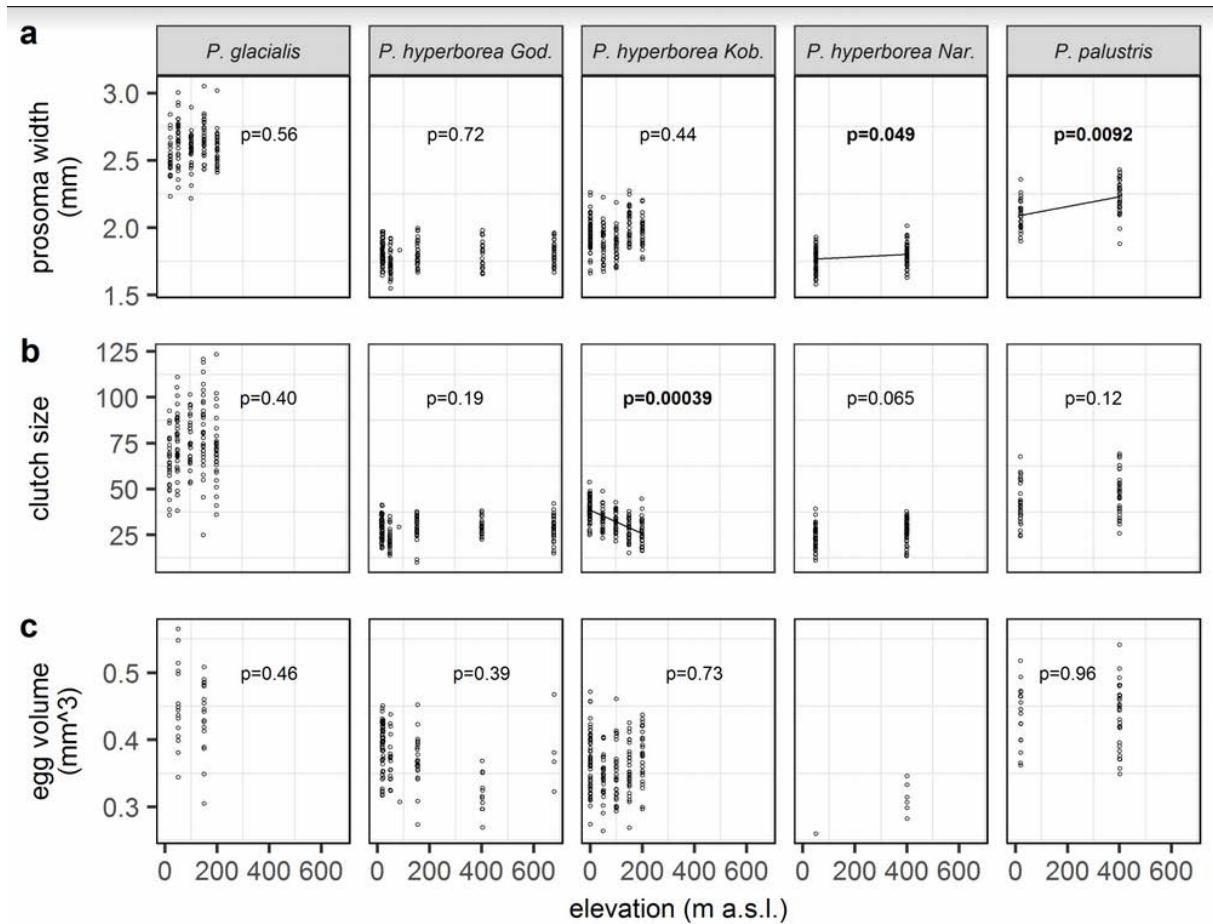
567

		Initial model	Model	Response variable	<i>F</i>	<i>D.f.</i>	<i>R</i> ²	<i>p</i>	Explanatory variables	<i>F</i>	<i>p</i>
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

570 **Fig.1** Map of the collecting sites of *Pardosa* species. From North to South: Zac: Zackenberg (74.467N,
 571 20.566W), Ice: Iceland (64.700N, 21.500W), God: Godthaabsfjord (64.144N, 51.474W), Kob:
 572 Kobbefjord (64.117N, 51.350W), Far: Faroe Islands (62.041N, 6.877W), Nar: Narsarsuaq (61.183N,
 573 45.371W). Latitude and longitude in Decimal Degrees WGS84.

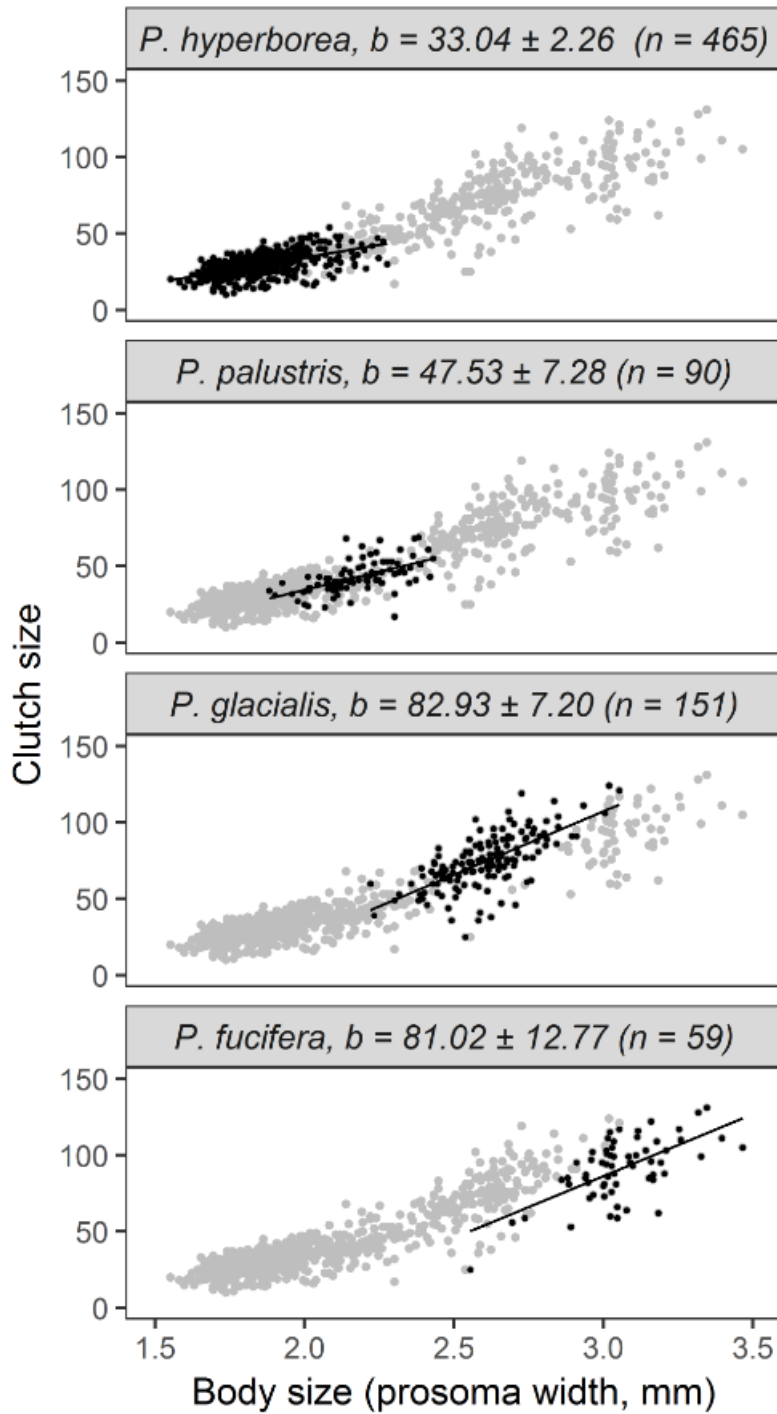


574

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

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

577 test ($n = 5$). Significant values are written in bold. Applied models are detailed in Table 3



578

579 **Fig.3** Linear regression results of clutch size on female size. Formulas are written as follows: $y = a +$
 580 $b * x$. *Pardosa hyperborea*: LLSR, clutch = $-31.68 + 33.04 * \text{size}$, $F_{445} = 212.7$, $R^2 = 0.32$, $p < 0.0001$, *P.*
 581 *palustris*: LSSR, clutch = $-60.52 + 47.53 * \text{size}$, $F_{88} = 42.67$, $R^2 = 0.32$, $p < 0.0001$, *P. glacialis*: LLSR,
 582 clutch = $-141.42 + 82.93 * \text{size}$, $F_{149} = 132.7$, $R^2 = 0.47$, $p < 0.0001$, *P. fucifera*: LLSR, Clutch = -159.28
 583 $+ 81.02 * \text{prosoma width}$, $F_{57} = 30.49$, $R^2 = 0.34$, $p < 0.0001$

584

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.)
<i>P. glacialis</i>	Thorell 1872	Holarctic ^[20] , Nearctic, Arctic, Greenland (G) ^[21]	not specified	0-860 ^[13,14,15]
<i>P. hyperborea</i>	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]
<i>P. furcifera</i>	Thorell 1875	Canada, Alaska, Greenland (S, SW ^[21]), Iceland ^[20] . trans-Nearctic arcto-alpine range ^[10, 21]	not specified	0-1360 ^[13,14,15]
<i>P. palustris</i>	Linnaeus 1758	Holarctic ^[20]	generalist ^[7] (widespread, especially in cold climates) ^[1]	up to 2500 ^[2,7,9,11]

Species	Found habitats
<i>P. glacialis</i>	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]
<i>P. hyperborea</i>	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 of jack 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]
<i>P. furcifera</i>	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 <i>Salix herbacea</i> snow beds as well as in the moss layer of heaths adjoining brooks. Also in herb fields on slopes and in <i>Salix glauca</i> thickets ^[21]
<i>P. palustris</i>	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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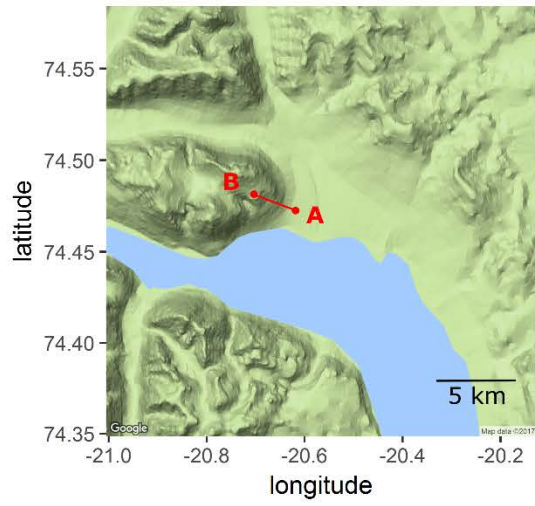
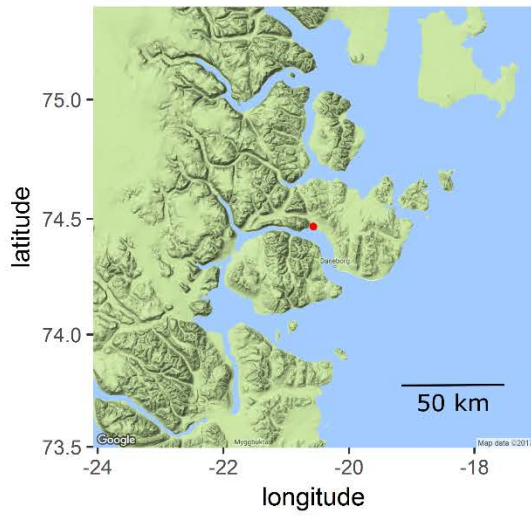
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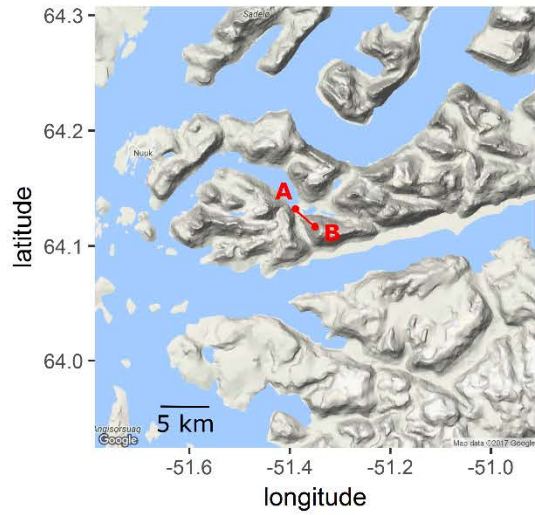
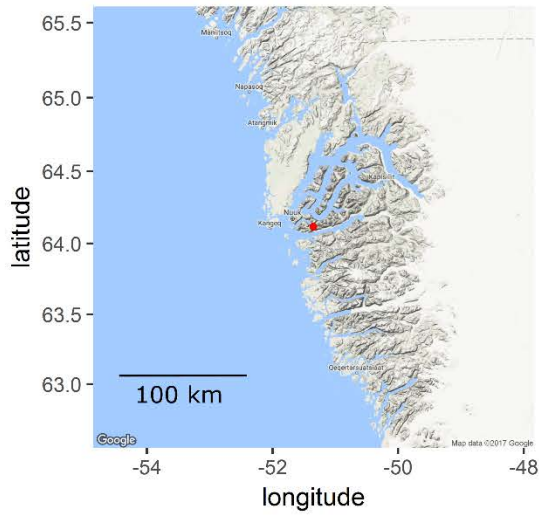
Corresponding author: cameline8@gmail.com

Online Resource 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.

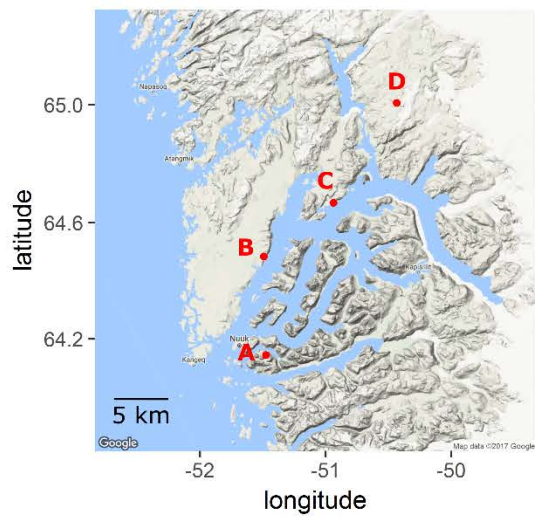
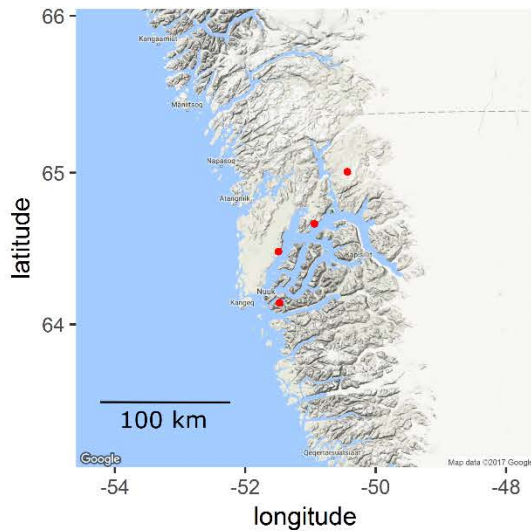
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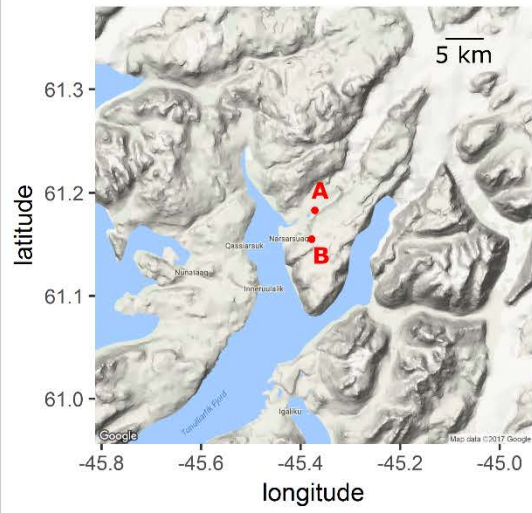
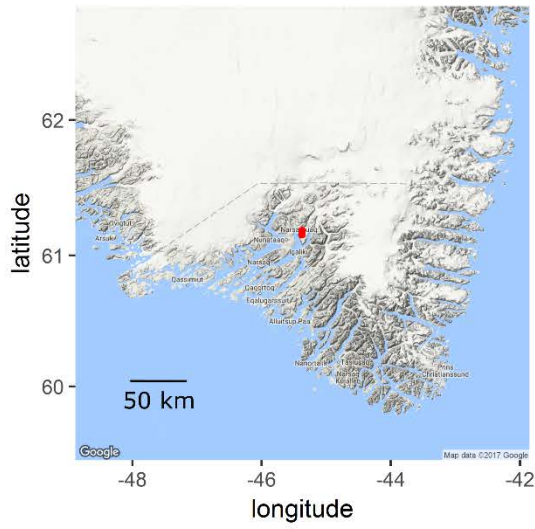
Kobbefjord



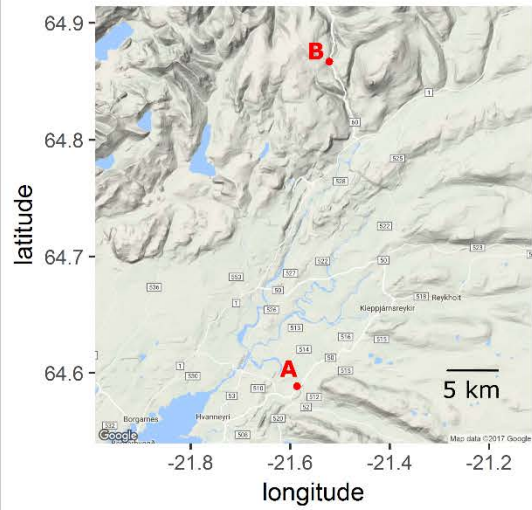
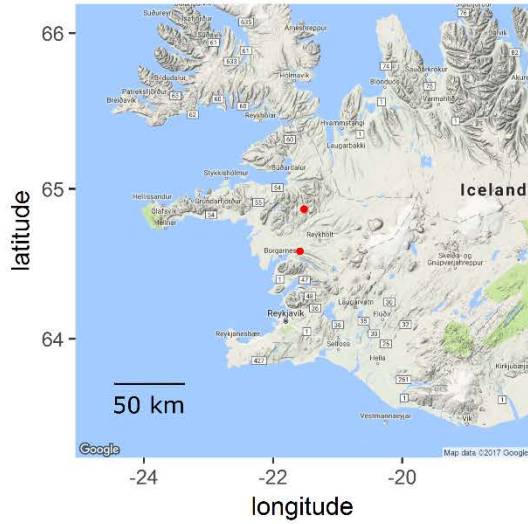
Godthaabsfjord



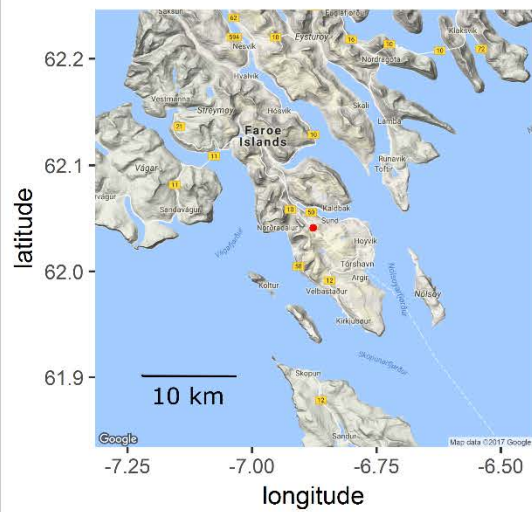
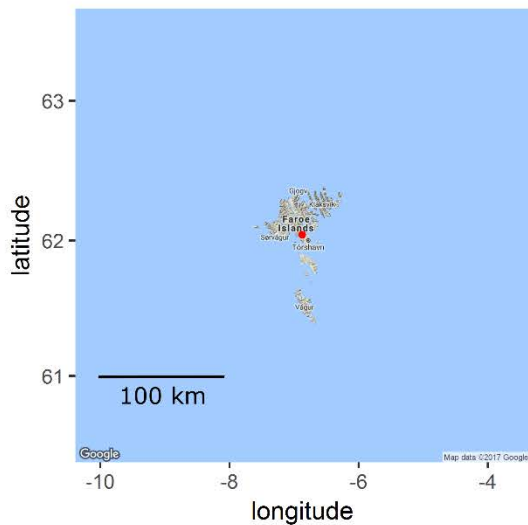
Narsarsuaq



Iceland



Faroe Islands



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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

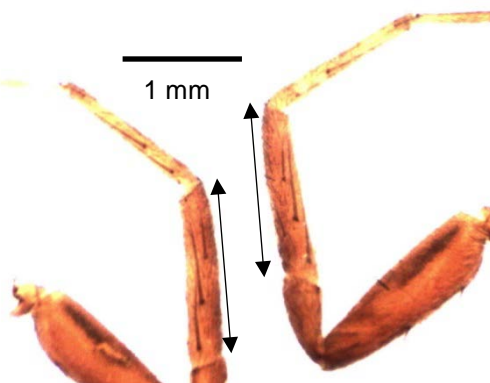


Fig.1.2 Leg 1's tibias measurement

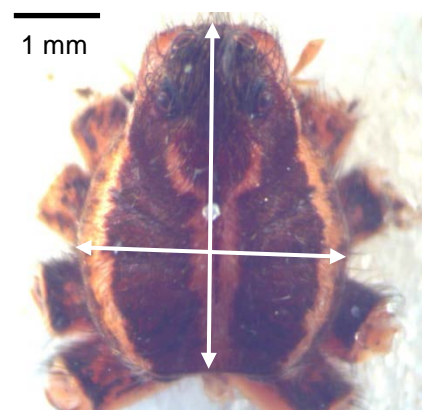


Fig.1.3 *P. furcifera*'s prosoma



Fig.1.4 *P. glacialis*' prosoma

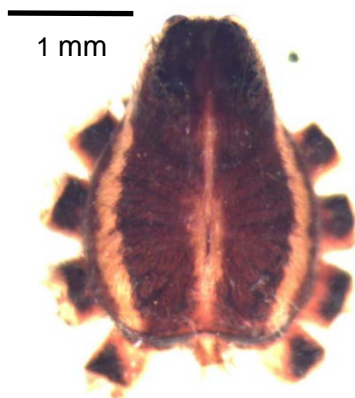


Fig.1.5 *P. palustris*' prosoma

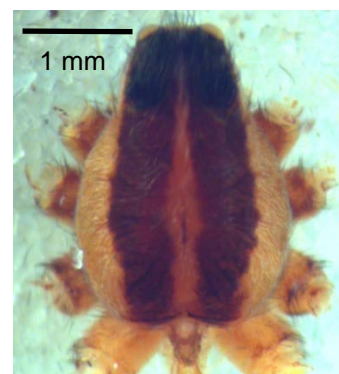


Fig.1.6 *P. hyperborea*'s prosoma



Fig.2.1 Parasitoid larvae in egg sac

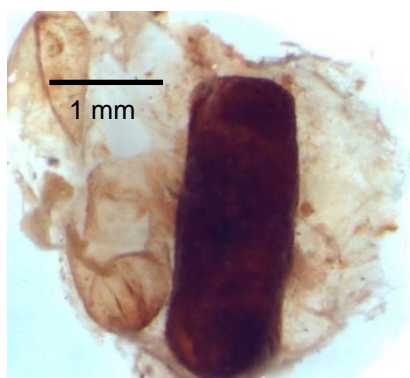


Fig.2.2 Parasitoid pupae in egg sac



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

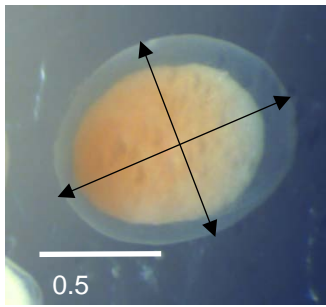


Fig.3.1 Egg development stage I



Fig.3.2 Stage I

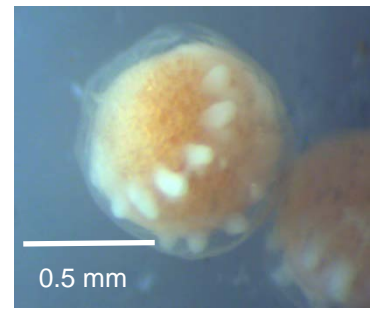


Fig.3.3 Stage II



Fig.3.4 Stage II

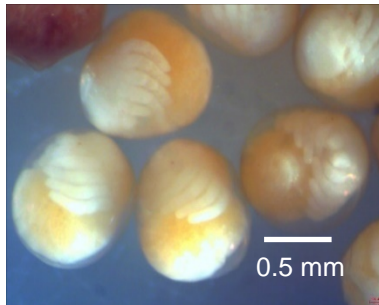


Fig.3.5 Stage III

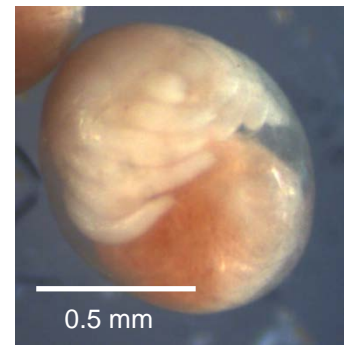


Fig.3.6 Stage III



Fig.3.7 Stage IV



Fig.3.8 Stage V

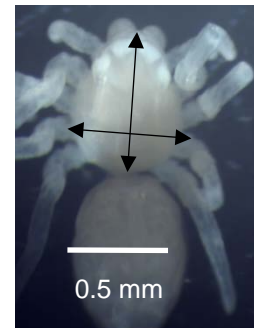


Fig.3.9 Stage V



Fig.3.10 Stage V

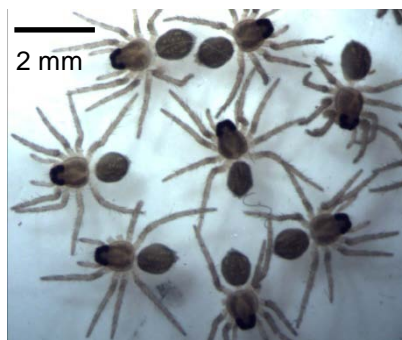
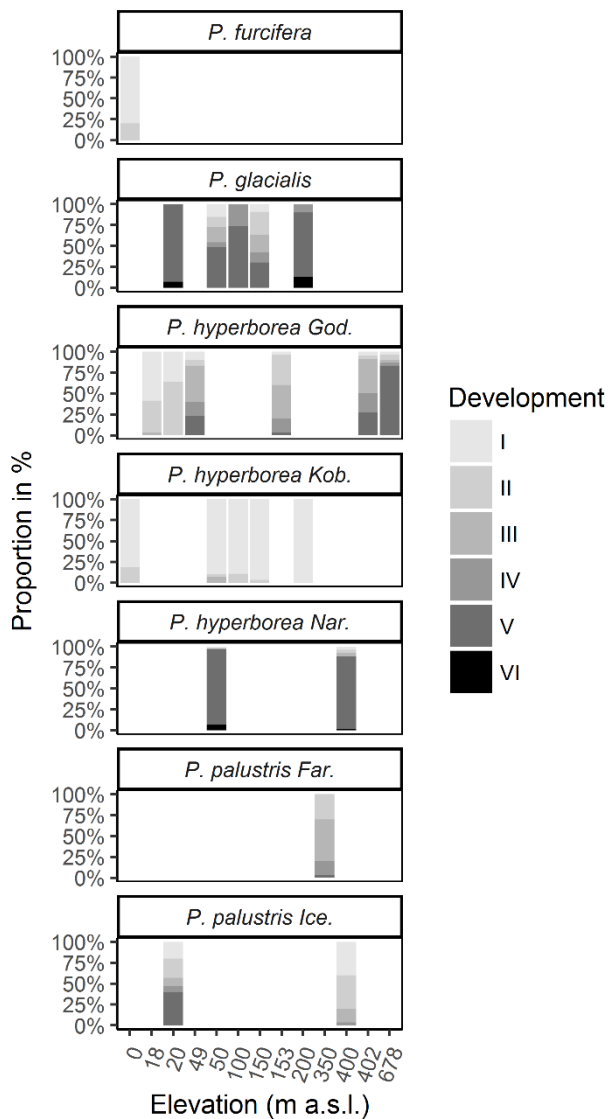


Fig.3.11 Stage VI



Fig.3.12 Stage VI

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.



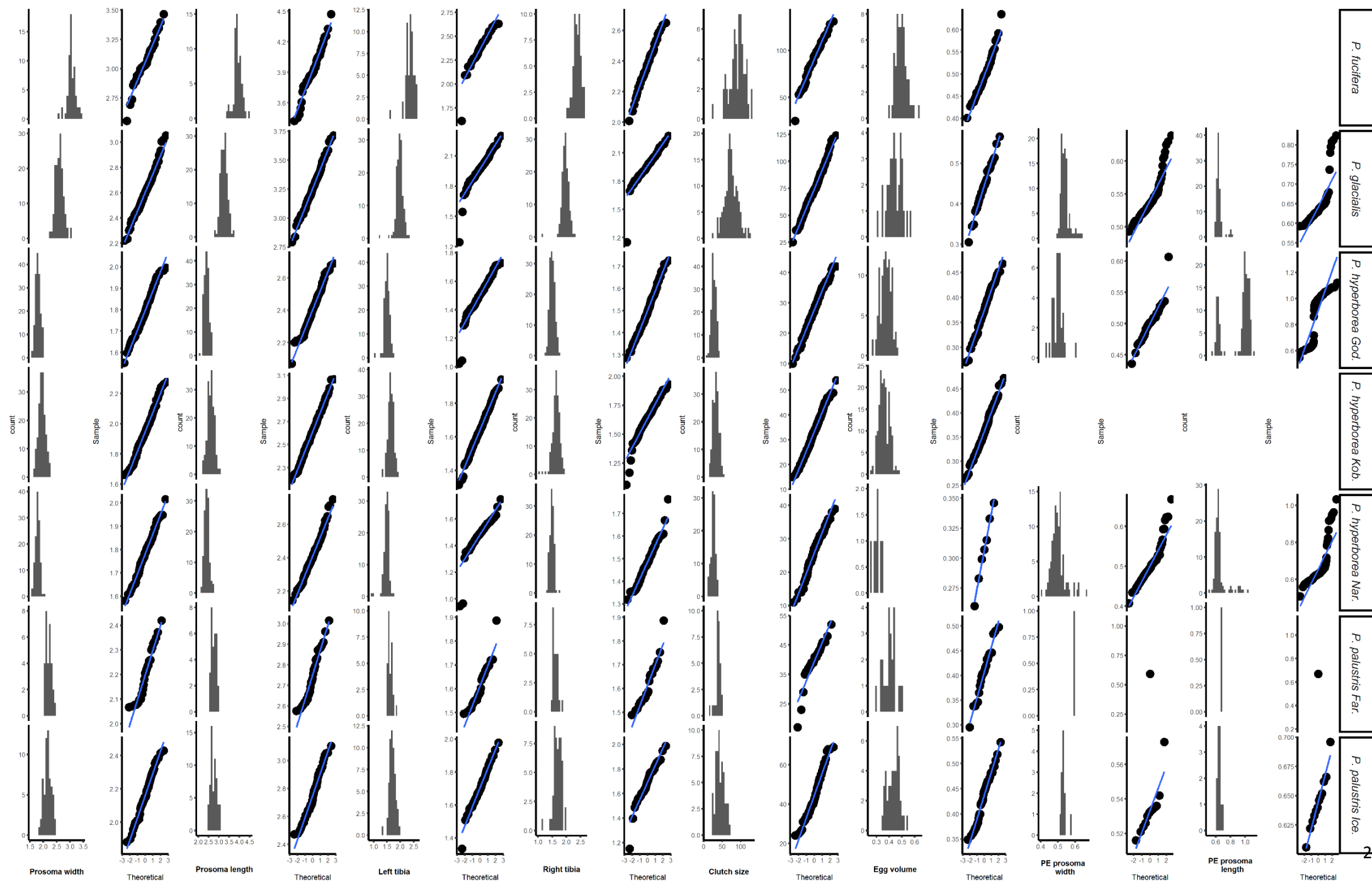
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Online Resource 5 Fig. 1: Normal distribution of the measured variables. Histograms show the distribution of the measured variable. Corresponding panels on the right show Quantile-Quantile plots (x-axis: Theoretical quantiles, y-axis: Sample quantiles). 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. tuctiera

P. glacialis

P. hyperborea God.

P. hyperborea Kob.

P. hyperborea Nar.

P. palustris Far.

P. palustris Ice.

2