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1 **Multiple reproductive events in female wolf spiders *Pardosa hyperborea* and**  
2 ***P. furcifera* in the Low-Arctic: one clutch can hide another**

3

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11 **ABSTRACT**

12 Changing abiotic conditions can affect the phenology of animals and plants with implications  
13 for their reproductive output, especially in rapidly changing regions like the Arctic. For instance  
14 in arthropods, it was recently shown that females of the spider species *Pardosa glacialis*  
15 (Thorell, 1872) (Lycosidae) are able to produce two clutches within one growing season in  
16 years when snowmelt occur particularly early. This phenomenon could be widespread in  
17 northern latitudes, and here we investigated the voltinism of two other very abundant species  
18 of wolf spiders in the Low-Arctic, *Pardosa hyperborea* (Thorell, 1872) and *Pardosa furcifera*  
19 (Thorell, 1875), over the period 2015 – 2017. While a bimodal pattern in the clutch size  
20 frequency distribution was only revealed for *P. hyperborea*, we were able to show that both  
21 species can produce a second clutch over the active season by using information on the  
22 embryonic stages. We also observed significantly larger first than second clutches. We argue  
23 that information about the embryonic stage can be critical for evaluating evidence of wolf spider  
24 populations producing more than one clutch in a season. Our study provides evidence that  
25 bivoltinism could be more widespread pattern than expected in Arctic wolf spiders. It remains  
26 to be investigated what the trophic consequences of such patterns are in a global warming  
27 context. We thus highlight the need for a coordinated framework for such further studies,  
28 integrating and relating various functional traits.

29 **Keywords:** Voltinism, Life-history traits, South-Greenland, Lycosidae, Phenology, Fitness

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35 interest.

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

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

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

## 44 INTRODUCTION

45 The Arctic is known to warm at a high rate (IPCC 2019), and several biological  
46 consequences have already been reported like shrub encroachment, northward expansion of  
47 insect herbivores or shifting phenologies (Post et al. 2009). This region, defined as the  
48 bioclimatic zone north of the climatic limit of trees and characterised by a tundra vegetation  
49 (CAFF 2013, 2021), is considered ideal for monitoring biological responses to environmental  
50 variation across space and time because of the various and especially strong abiotic gradients  
51 shaping the landscapes (Hansen et al. 2016). Within the last decades, studies have documented  
52 abundance trends and species assemblages across Arctic habitats, especially focusing on  
53 arthropods (e.g. Høye et al. 2018). Recent phenological studies have brought precious insights  
54 about the importance of these organisms in the Arctic food web (e.g. Leung et al. 2018) and  
55 about arthropod activity in relation to climate (e.g. Kankaanpää et al. 2018).

56 Numerically dominating a highly interconnected trophic web (Schmidt et al. 2017),  
57 terrestrial arthropods are generally known to respond quickly to several environmental changes  
58 (Spiller et al. 2017) and therefore constitute suitable study models. Wolf spider species are  
59 particularly relevant for such purpose (Marusik and Koponen 2002), because of their  
60 importance in ecological communities as prey and predators (Schmidt et al. 2017), and because  
61 they are ubiquitous, being present in high densities in many habitats (Jocqué and Alderweireldt  
62 2005). In the temperate zone, wolf spider life-cycles and patterns of voltinism are well  
63 documented (e.g. Brown et al. 2003), contrary to higher altitudes and northern latitudes (e.g.  
64 Bowden and Buddle 2012b). *Pardosa* species, for example, have one generation a year in the  
65 temperate zone, females often producing more than one clutch (i.e. egg sac), while they would  
66 require more time to complete their development in the colder parts of the Arctic (Ameline et  
67 al. 2017). Buddle (2000) and Pickavance (2001) described in five boreal/sub-Arctic *Pardosa*  
68 species a biennial life-cycle model characterised by individuals being juveniles and sub-adults

69 two winters in a row, and maturing as adults the third active season where individuals breed  
70 and die. In the Arctic, it has been assumed that female wolf spiders are only able to produce  
71 one clutch per lifetime because of the harsh conditions of the region (Bowden and Buddle  
72 2012a; but Hein et al. 2018). Indeed, extreme low temperatures and short active seasons limit  
73 the available time for organisms to mature and reproduce (Roff 1980; Høye et al. 2009).  
74 However, Høye et al. (2020) recently showed that in the High-Arctic (*sensu* CAFF 2013) at  
75 Zackenberg, NE Greenland, the wolf spider species *Pardosa glacialis* Thorell 1872 was able to  
76 produce a second clutch during the same season. This phenomenon could be more widespread  
77 than expected, and other wolf spider species from lower northern latitudes could already present  
78 a second phase of clutch production. This lack of fundamental knowledge points out the need  
79 for more basic research about arthropods life-history and ecology in the Arctic (Høye 2020).

80 In this paper, we investigate the voltinism of the two most abundant spider species of  
81 Low-Arctic areas in Greenland (Høye et al. 2018), *Pardosa hyperborea* and *Pardosa furcifera*,  
82 for the period 2015 - 2017. We predict that these species are able to produce a second clutch in  
83 one active season, like their High-Arctic congeneric *P. glacialis*. We also review the method  
84 described in Høye et al. (2020) for detecting second clutches and advocate for the use of more  
85 functional information like the embryonic stage when studying the reproductive phenology of  
86 wolf spider species.

87

## 88 MATERIAL AND METHODS

89 The study area is located near Narsarsuaq, South Greenland (61.16°N, 45.40°W) in the  
90 Sub-Arctic/Low-Arctic transition zone. This area can be defined as a transition zone between  
91 the northernmost part of the boreal zone, the “forest tundra”, and the southernmost part of the  
92 Arctic where the herbaceous vegetation cover is continuous and where shrubs are frequent  
93 (CAFF 2013). The experimental design (see Høye et al. 2018 for more details) consisted in

94 transects of yellow pitfall traps of 10 cm in diameter, containing a 50% propylene glycol:water  
95 mixture. Transects have been set-up in the two most representative habitats of the study area,  
96 i.e. (i) either in fen habitats as 40 m × 5 m rectangles, consisting in two rows of 9 pitfall traps  
97 five meters apart, or (ii) in shrub habitats as 20 m × 5 m rectangles, consisting in two rows of 5  
98 pitfall traps five meters apart. The limited size of shrub patches at the study site did not allow  
99 for making them as large as fen transects (Høye et al., 2018). In total, in each habitat type, three  
100 transects have been set up at 50 m above sea level, and two transects have been set up at 450 m  
101 above the sea level. The traps were collected weekly during the growing seasons of the period  
102 2015 - 2017. In this study, samples from only one transect line in each plot have been used, and  
103 analyses have been kept basic, e.g. not considering elevation or habitat influence, to primarily  
104 focus on phenological general trends over the 3-years period.

105 In the laboratory spiders were identified to the species level and samples containing  
106 female wolf spiders were kept separate with their egg sac if any whenever possible. Among the  
107 four wolf spider species collected (see Høye et al. 2018), only *P. furcifera* and *P. hyperborea*  
108 were retained for analyses as they were by far the most abundant species at the site (Høye et al.  
109 2018). Clutches were opened, the content was counted and the embryonic stage of the pulli was  
110 reported in two stages (after Ameline et al. 2018): “A”: the prosoma is not visible or is  
111 developing, i.e. early embryonic stage, and “B”: the postembryonic individual is hatched within  
112 the egg sac, i.e. late embryonic stage. Specimens are preserved in 75% ethanol and stored at the  
113 Natural History Museum Aarhus, Denmark (Høye et al. 2018).

114 In order to investigate the voltinism of the studied species, two methods were used for  
115 a comparative purpose. The first one, used by Høye et al. (2020a), consisted in plotting the  
116 frequency distribution of the clutch sizes (i.e. the number of eggs per clutch). The second one,  
117 the method we are proposing here, is based on the embryonic stage information. Firstly, the  
118 distribution of the clutch size was plotted against the week of the year, i.e. against the week of

119 collecting, according to the embryonic stage (“A” or “B”, see above). Then, the number of  
120 clutches per week was plotted for each embryonic stage and a corresponding smoothing curve,  
121 using the loess method, was drawn (package “ggplot2”: Wickham 2016). These last plots were  
122 used to split potential clutch phases without invoking a separation based on the clutch size.

123 All analyses were performed with the software R v.3.6.2 (R Core Team 2019).

124

## 125 **RESULTS**

126 The frequency distribution method revealed a clear bimodal distribution for *P.*  
127 *hyperborea* (Fig. 1a). In other words, this species showed two distinct peaks of clutch size with  
128 a split at 15 eggs. Over the 1393 clutches, 973 containing more than 15 eggs would be assigned  
129 to a first laying episode, and 420 containing 15 eggs or less would be assigned to a second  
130 laying episode. However, the clutch size distribution of *P. furcifera* did not show a similar  
131 pattern. We gathered the clutches into size classes of five (Fig. 1b) to reduce potential noise  
132 from the wide range of clutch sizes in this species (from 14 to 177 eggs per clutch). However,  
133 this plot did not display any bimodal trend either. Therefore, this method indicates a single  
134 phase of clutch production for *P. furcifera*.

135 From the embryonic stage method, the clutch size distribution over time showed two  
136 main results for both species (Fig. 2a,b). Firstly, the distribution across the season indicated a  
137 trend towards smaller clutches near the end of the sampling period. Secondly, a relatively clear  
138 pattern appeared when looking at the embryonic stage for both species: (i) the plots showed a  
139 majority of early embryonic stage clutches (i.e. stage A), followed by a period of late embryonic  
140 stage clutches (i.e. stage B), itself followed by a second occurrence of early embryonic stage  
141 clutches. To clarify what seemed to be two phases of clutch production, we plotted the number  
142 of clutches collected over time (Fig. 2c,d). For both species, the smoothing curves of the early



143 embryonic stage supported the idea of two laying episodes, which would split between week  
144 31 and 32. However, no specific pattern was observed for the late embryonic stage. Therefore,  
145 considering the first embryonic stage of the pulli this method indicated (i) a first laying episode  
146 between the weeks 24-31 and 25-31 for *P. hyperborea* and *P. furcifera*, respectively, and (ii) a  
147 second laying episode between the weeks 32-36 and 32-35 for *P. hyperborea* and *P. furcifera*,  
148 respectively. Furthermore, to test the trend of declining clutch sizes over the season, we  
149 performed a Generalised Linear Model using a negative binomial distribution, and an ANOVA  
150 test for each species. Regardless of the embryonic stage, we found a significant difference in  
151 mean clutch size between the two time periods for *P. hyperborea* ( $23.54 \pm 0.26$  mm,  $n = 922$   
152 vs.  $13.58 \pm 0.24$  mm,  $n = 471$ ; Log-likelihood ratio test:  $\text{Chisq} = 693.4$ ,  $df = 1$ ,  $p < 0.0001$ ) and  
153 for *P. furcifera* ( $87.07 \pm 2.55$  mm,  $n = 150$  vs.  $63.37 \pm 2.60$  mm, Log-likelihood ratio test:  $\text{Chisq}$   
154  $= 38.57$ ,  $df = 1$ ,  $p < 0.0001$ ).

155

## 156 **DISCUSSION**

157 We found that both species of wolf spiders in this study exhibit two distinct phases of  
158 clutch production over time, which supports our hypothesis that the ability to produce more  
159 than one clutch is widespread, not only in the temperate zone but also in northern latitudes. This  
160 pattern is particularly striking when looking at the early embryonic stage of the pulli, i.e. when  
161 clutches mainly contain eggs. The clutches with later embryonic stage should follow the same  
162 temporal progression, but in our data this pattern was less clear. This could be due to  
163 development differences between clutches inducing an overlap of the phases, e.g. a slow  
164 development of the pulli from the beginning of the season concomitant with a faster  
165 development of the pulli from the middle of the season, as arthropods development is  
166 particularly sensible to factors like temperature (van der Have and de Jong 1996). However, it  
167 is more likely that our sampling stopped before the effective end of the active season and that

168 we missed the second peak of the late embryonic stage. Indeed, local weather readings usually  
169 display positive average temperatures 3 to 4 weeks after our last pitfall trap collection (5-10 °C  
170 on average between weeks 37 to 39 for the years 2012-2016; Høye, unpubl. data).

171 *Pardosa* species (e.g. Eason 1969) as others wolf spiders (e.g. Brown et al. 2003) are  
172 known to produce more than one clutch per lifetime in temperate latitudes. Høye et al. (2020)  
173 showed a similar pattern in High-Arctic Greenland (at Zackenberg). It is therefore not surprising  
174 to observe the same phenomenon at these lower latitudes. Nevertheless, it is the first time that  
175 a bivoltinism pattern is clearly demonstrated for spiders in the Low-Arctic. This represents a  
176 valuable addition of information to the many knowledge gaps about the ecology of most  
177 arthropod species of this region (Høye 2020).

178 Plasticity in voltinism has previously been reported in arthropods (e.g. Jönsson et al. 2009) for  
179 which environmental and climatic factors are decisive parameters mediating their life-cycle  
180 (Horne et al. 2015). In the Arctic, timing of snowmelt plays a substantial role for the ground-  
181 dwelling animals, e.g. by initiating the active season for many species (Høye et al. 2009;  
182 Kankaanpää et al. 2018). In *P. glacialis* (Høye et al. 2020), earlier snowmelt would allow  
183 females to produce their first clutch earlier, which would give them enough time to produce a  
184 second clutch before the season ends. Given the harsh conditions of the Arctic, it is likely that  
185 *P. hyperborea* and *P. furcifera* are also adapted to quickly respond to favourable conditions by  
186 modulating their voltinism over space and time. More specifically, while climatic conditions  
187 are fluctuating from one year to the next, the ability to rapidly take advantage to favourable  
188 conditions, i.e. showing a plasticity in the reproduction, might have been selected over time. As  
189 conditions like temperatures are likely becoming less severe with the current warming, the trend  
190 we describe here could become more frequent, and more pronounced in the coming years.  
191 Future studies could further examine how spatial environmental gradients (e.g. temperature and

192 moisture) that characterise Arctic landscapes (Hansen et al. 2016) may affect patterns of  
193 voltinism.

194 It is noteworthy that we would not have been able to identify the second clutches in *P.*  
195 *furcifera* without information about the embryonic stages. While the frequency distribution  
196 method proposed by Høye et al. (2020) is easy to apply and to explain, and doable with  
197 relatively little information, it did not catch the expected pattern for *P. furcifera*. This method  
198 might not be sufficiently precise to unravel intraspecific variations from an actual phenological  
199 trend in a more complex situation where abiotic factors (e.g. environmental and climatic  
200 parameters) are probably influencing the clutch size. Indeed, the clutch size has been observed  
201 to decline over laying episodes (e.g. Eason 1969; Buddle 2000), probably because the females  
202 have a limited amount of energy to allocate for reproduction, mostly invested in the first clutch  
203 (i.e. the so-called size-number trade-off, e.g. Marshall and Gittleman 1994; Hein et al. 2018).  
204 For these reasons, we recommend using the embryonic stage as complementary to the frequency  
205 distribution method when studying wolf spiders life-histories. It seems to be a more precise  
206 indicator and it does not require a substantial additional lab workload.

207 More broadly, we support the measurement and the consideration of more functional  
208 predictors, i.e. functional traits (Violle et al. 2007), many traits being related such as the  
209 maternal body size that is directly affecting the number of produced offspring in spiders (e.g.  
210 Simpson 1995; Ameline et al. 2018). A more mechanistic approach would allow to better  
211 understand the interactions between the species and their environment over space and time  
212 (Bartomeus et al. 2013; Moretti et al. 2017). While it remains unclear if an increased  
213 reproductive rate leads to increasing fitness (Høye et al. 2020), as additional cocoons might be  
214 unfertilised or not viable, rising temperatures could result in higher wolf spider densities in the  
215 Arctic tundra (Entling et al. 2010; Ameline et al. 2018). An increased population growth would  
216 probably affect the whole trophic web (e.g. Eitzinger et al. 2019), altering intra- (e.g.

217 cannibalism - Koltz and Wright 2020) and inter-specific interactions (e.g. parasitism - Koltz et  
218 al. 2019), or even processes like carbon cycle feedbacks (e.g. litter decomposition - Koltz et al.  
219 2018). Such issues highlight the importance of a coordinated framework for ecologists and  
220 evolutionary biologists working on arthropods, favouring a more efficient and standardised  
221 collection, management and treatment of data in a long-term research perspective (Høye and  
222 Culler 2018; Lowe et al. 2020).

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342

343 **FIGURE LEGENDS**

344

345 **Fig. 1** Frequency distribution of clutch sizes in the wolf spiders *Pardosa hyperborea* (**a**) and  
346 *P. furcifera* with clutches grouped into size classes of five (**b**), across respectively 1393 and  
347 229 clutches collected in pitfall traps at Narsarsuaq (Greenland) during the period 2015 –  
348 2017. The solid lines represent locally weighted smoothing with span parameters = 0.5 and  
349 identifies in *P. hyperborea* a local minimum at a clutch size of 15 eggs, implying two laying  
350 episodes, as indicated by the grey vertical hatched line.

351

352 **Fig. 2** Clutch size distribution and number of clutches collected over weeks of year for the  
353 wolf spiders *Pardosa hyperborea* (**a** and **c** respectively) and *P. furcifera* (**b** and **d**  
354 respectively) according to the embryonic stage (black line and dots for stage “A”; yellow line  
355 and triangles for stage “B”), from pitfall traps collected at Narsarsuaq (Greenland) during the  
356 period 2015 – 2017. The solid lines (**c** and **d**) represent locally weighted smoothing with  
357 default span parameters and identify local minimums between weeks 31-32 for both species,  
358 implying two phases of clutch production over time, as indicated by the grey vertical hatched  
359 lines.



