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

Nathan Viel[1,2,*], Cecilie Mielec[2], Julien Pétillon[1,3] and Toke T. Høye[2,4]

[1]Université de Rennes, UMR CNRS 6553 Ecobio, 35000 Rennes, France

[2]Aarhus University, Department of Ecoscience and Arctic Research Centre, Grenåvej 14, 8410 Rønde, Denmark

[3]https://orcid.org/0000-0002-7611-5133

[4]https://orcid.org/0000-0001-5387-3284

[*]Corresponding author; Email: pro.viel.nathan@gmail.com

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ABSTRACT

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

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

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DECLARATIONS

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Availability of data and material (data transparency)

Code availability (software application or custom code)

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

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INTRODUCTION

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

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

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

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

MATERIAL AND METHODS

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

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

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

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

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

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

RESULTS

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

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

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

DISCUSSION

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

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

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

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

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

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

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

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

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FIGURE LEGENDS

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

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

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