Habitat specialization and climate affect arthropod fitness: a comparison of generalist vs. specialist spider species in Arctic and temperate biomes

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Life history trade-offs are a key notion in evolutionary biology, notably for understanding how selection shapes the diversity of traits among species. Despite the frequent study of such trade-offs, few studies synchronously investigate the effects of multiple factors, such as niche specialization and adaptation to harsh environments. We compared reproduction (fecundity and egg quality) in two sympatric couples (one habitat generalist and one specialist) of congeneric wolf spider species, in both Arctic and temperate habitats. We found that specialist species at both latitudes invested more in clutch size than did generalist species. We interpret this result as an optimization of clutch production. In the Arctic, the specialist was able to invest in fecundity with increasing body size at a much higher rate than the generalist species. In the temperate habitat, both species showed similar strategies: they increased quantity and quality of offspring relative to body size at the same rate. These results are consistent with the hypothesis that Arctic species must develop distinct strategies in order not to overlap each other's ecological niches as a consequence of limited food resources or niche space. We emphasize the need to test the role of plasticity and environmentally mediated effects of competition on arthropod fitness.

ADDITIONAL KEYWORDS: body size – competition – latitude – life history – Lycosidae – *Pardosa* spp. – reproductive trade-offs – sympatric species.

INTRODUCTION

There is a stunning diversity of life histories among species. This diversity can be explained by life history theory, which proposes that life history trade-offs are shaped by natural selection in order to maximize fitness with a fixed amount of available resources for allocation to reproduction, or any other component at any given time (Stearns, 1992; Roff, 2002). In this context, a reproductive quality/quantity trade-off in the investment of resources related to female body size is often revealed (Brown, Sanford & Swerdon, 2003; Skow & Jakob, 2003; Bowden & Buddle, 2012a). With reproduction being such a large investment, it follows that trade-offs between quality and quantity are particularly relevant under harsh environmental conditions (e.g. limited resources due to competition or adverse abiotic conditions; Roff, 2002). In such sub-optimal conditions, the mother should increase the quality of her offspring while decreasing the number produced (Roff, 1993). Indeed, offspring fitness increases with investment per individual (Smith &

Fretwell, 1974). This explanation proposes that habitat constraints drive reproductive trade-offs, which are frequently studied along geographical or environmental gradients (Albuquerque, Tauber & Tauber, 1997; Reed & Nicholas, 2008; Liao, Lu & Jehle, 2014). In the context of community ecology, coexistence of similar/related species could be mediated by differing life history strategies (Tokeshi, 1999). Hence, a natural experiment taking advantage of congeneric coexisting species in environments differing in harshness could provide insight into the combined effects of abiotic and biotic factors on reproductive trade-offs.

In this study, we assessed and compared reproductive trade-offs between species contrasting in habitat specialization between two climates differing in harshness. In order to do so, we compared the relationship between female body size and reproductive traits (fecundity and egg quality) in two sympatric couples of congeneric wolf spider species (Lycosidae) composed of one generalist and one specialist collected from the Arctic (south-west Greenland) and a temperate habitat in Belgium and in the Netherlands. We used egg number and volume as proxies for fecundity and offspring quality, respectively. For Arctic wolf spider species, clutch size is considered as a proxy for fecundity because only one clutch per lifetime is likely produced (Bowden & Buddle, 2012b). In temperate *Pardosa* species, however, we acknowledge that some species produce one clutch per lifetime (Harvey, Nellist & Telfer, 2002; Puzin *et al.*, 2011), while others can produce up to two clutches per lifetime (Vlijm, Kessler & Richter, 1963; Alderweireldt & Maelfait, 1988; Bonte & Maelfait, 2001). The latter clutch is produced at a distinctive period of time, well after the first, with clutches typically being separated by several weeks (Bonte & Maelfait, 2001). Offspring quality was approximated with egg volume, as bigger eggs result in bigger and fitter offspring (Fox & Czesak, 2000). Female wolf spiders carry their egg sac tethered to their abdomen, allowing for the collection of data on the individual along with data on reproductive traits (e.g. Hendrickx *et al.*, 2003; Pétillon *et al.*, 2009). Using four congeneric species from two latitudes, we aim to evaluate three hypotheses about life history strategies between two groups of species differing in habitat specialization and geographic location.

Based on the literature related to life history theory and empirical work on wolf spiders, we make the following hypotheses: (1) fecundity will increase with female body size while egg quality will vary independently of female body size in all four species, as female size is related to fecundity, and female condition to offspring quality (Simpson, 1993; Puzin *et al.*, 2011; Bowden & Buddle, 2012a); (2) specialist species will have a relatively higher reproductive output than generalist species because they are supposed to be better adapted to their habitat; a higher reproductive output being reflected by the ability to invest in clutch size more than in egg volume (e.g. Pétillon *et al.*, 2009). Indeed, we suppose that if better adapted to their environment, the offspring of specialists would not need as much resources as the generalists' offspring; (3) finally, egg quantity/quality trade-offs are expected to be stronger in the Arctic than in the temperate habitat as trade-offs are more often detected in harsh habitats due to limited resources (Roff, 2002).

MATERIAL AND METHODS

FOCAL SPECIES AND SITES

We hand collected four different species of wolf spiders (*Pardosa* spp.) as two couples of sympatric species in distinct habitats, each couple being composed of one generalist and one specialist species. *Pardosa hyperborea* (Thorell, 1872) ($n = 60$), generalist and *P. furcifera* (Thorell, 1875) ($n = 60$), specialist were collected in an Arctic habitat, whereas *P. amentata* (Clerck, 1757) ($n = 65$), generalist and *P. agricola* (Thorell, 1856) ($n = 68$), specialist were collected in a temperate habitat. Details of the species' ecology are given in Table 1. As stated in Table 1, we considered *P. hyperborea* as a generalist species and *P. furcifera* as a specialist species. Indeed, in a previous study (unpublished data), we could abundantly find the former in three locations in south-west Greenland, from 0 to about 700 m a.s.l., although we could only find the latter in one of these locations, abundantly at sea level (60 individuals sampled) but very rarely at high elevation (three individuals found at 200 m a.s.l.).

Collections were conducted in dwarf shrub heath habitats in Kobbefjord (64.117N, 51.350W), Greenland, from 5 to 10 July 2013, and along the river banks of the Common Meuse separating Belgium and the Netherlands (51.000N, 5.800E) on 1 June 2005 and 8 June 2006. From each site, a minimum of 30 females with egg sacs were collected for both populations within the same relatively small area (~1 km^2) and preserved individually in 70% alcohol. Further sampling details are presented in Supporting Information Table S1.

MEASUREMENTS IN LABORATORY

Fecundity and egg quality were measured using clutch size and egg volume as proxies, respectively. Measurements were done to the nearest 0.01 mm via digital photographs using EUROMEX ImageFocus v3.0 (Arctic samples) or directly with a measuring ocular using a WILD M5 stereomicroscope (temperate samples). For each individual, we measured the width of the prosoma, and counted the eggs in the sac. We also measured mean length and width of ten eggs

Table 1. Description of the four species collected on the field

Species	Description	Distribution	Elevation (m a.s.l.)	Habitat specialization
P. hyperborea	Thorell, 1872	Holarctic[20]	100–1360[3,4,13,14,15,16,17]	Generalist
P. furcifera	Thorell, 1875	Canada, Alaska, Greenland, Iceland[20]: trans-Nearctic arcto-alpine range[11]	0–1360[14,15,16]	Specialist
P. amentata	Clerck, 1757	Europe, Russia[20]	Up to 2300 [3,8,17,19]	Generalist
P. agricola	Thorell, 1856	Europe to Kazakhstan[20,19]	Not in elevated regions 0–500 [18,19]	Specialist

Species	Found habitats
P. hyperborea	Open forests and moors[19], birch wood[2,16], sphagnum bogs (in boreal zones[9]), 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[5], transition boreal forest to Arctic tundra[15], subarctic pine forest area, birch woods, bogs and treeless fells[16]
P. furcifera	Spruce-pine forests, in willow clumps near the timberline, and on moss and stones in alpine tundra[5], subarctic pine forest area, birch woods, bogs/heath transitions and treeless fells[15,16]
P. amentata	Widespread in damp habitats[6,19,21], lowlands[12] and mountains above the forest-line[7], tundra[17], rich grassland, poor grassland, ash woodland[10], marshy hollow with stream and willow scrub above the birch tree-line[3]
P. agricola	In open, sandy terrain, in stony banks of lakes and watercourses[1,19], on wet moss by the shore [3]

References: 1: Vlijm, 1971; 2: Bengston *et al.*, 1976; 3: Ashmole & Planterose, 1979; 4: Koponen, 1987; 5: Dondale & Redner, 1990; 6: Buchar, 1993; 7: Deltshev, 1995; 8: Logunov, Marusik & Koponen, 1998; 9: Koponen, 2002; 10: Cameron, Johnston & McAdam, 2004; 11: Marusik, Böcher & Koponen, 2006; 12: Fet & Popov, 2007; 13: Hammel & Nickel, 2008; 14: Høye & Hammel, 2010; 15: Bowden & Buddle, 2010; 16: Koponen, 2011; 17: Hein *et al.*, 2014; 18: British Arachnological Society, 2015; 19: Nentwig *et al.*, 2015; 20: World Spider Catalog, 2015.

randomly taken from each clutch. Mean egg volume was then calculated as the mean of their volume using the formula: Volume $= \frac{\pi}{6} \times \text{length} \times \text{width}^2$ (mm³) following Hendrickx & Maelfait (2003). In the situation where eggs had hatched inside the egg sac ($n = 34$ out of 65 *P. amentata* females and $n = 22$ out of 68 *P. agricola* females), we measured the prosoma of ten postembryonic individuals (i.e. nymphs) as a proxy for egg volume. Since a female was always collected with an intact egg sac, we assume not to have lost any postembryonic individual.

As sampling was not necessarily done at the same stage of egg development, we considered mean egg volume as a less reliable trait than clutch size. We consequently did not use a variable connecting clutch size and mean egg volume, but instead used them separately as response variables in our models.

ANALYSES

We assessed the effect of body size on reproductive traits (clutch size and mean egg volume or mean body size of postembryonic individuals) for the two couples of sympatric species.

The distribution of measurements was plotted and normality was tested via a distribution histogram and a quantile-quantile plot. All measured variables were normally distributed. Comparisons were performed via one-tailed *t*-tests, ANOVA or Kruskal–Wallis models after testing for homoscedasticity. Correlations between traits were assessed with Pearson tests.

We used ANCOVA models for the analyses and Linear Least Squares Regressions (LLSR) for the graphical representations of the significant effects in the models. For each initial model, we selected the model with the lowest Akaike Information Criterion (package 'MASS': Venables & Ripley, 2002). The significance of explanatory variables and factors was then tested using ANOVA and type III sums of squares (package 'car': Fox & Weisberg, 2011), that is without taking into account the order of the explanatory variables/factors. All non-significant interactions and factors were excluded from the final models. Finally, we tested if the residuals of the final model were normally distributed and this was done via a distribution histogram and a quantile-quantile plot. A significant effect is referred in the text as an 'effect of the variable/factor on the other variable'.

All means are presented with standard deviation (package 'RVAideMemoire': Hervé, 2015) and all statistics were conducted with the R v. 3.1.3 software (R Development Core Team, 2014) and Microsoft Excel (2013).

RESULTS

COMPARISON OF SYMPATRIC SPECIES IN THE ARCTIC BIOME

The mean body size of the generalist species (*P. hyperborea*) was 1.85 ± 0.13 mm ($n = 60$), while the mean body size of the specialist species (*P. furcifera*) was 3.05 ± 0.14 mm ($n = 59$, one specimen was dry and consequently not usable). Our results show an effect of species and a positive effect of female body size on clutch size, which differed between the two species (Table 2, Fig. 1A). Indeed, the specialist species increased clutch size at a higher rate than the generalist species when body size increased, as the regression slopes were 81.93 and 36.63, respectively (Fig. 1A). Mean clutch size of *P. hyperborea* and *P. furcifera* was 39 ± 6 ($n = 60$) and 91 ± 19 ($n = 59$), respectively and was significantly higher in *P. furcifera* (one-tailed *t*-test, $t = 19.48$, d.f. $= 69.76$, $P < 2.2 \times 10^{-16}$). Our results showed an effect of species on mean egg volume, but no effect of female body size (Table 2). Mean egg volume for *P. hyperborea* and *P. furcifera* was 0.37 ± 0.04 mm^3 ($n = 60$) and 0.50 ± 0.04 mm^3 ($n = 59$), respectively and was significantly higher for *P. furcifera* (one-tailed *t*-test, $t = 16.45$, d.f. $= 117$, $P < 2.2 \times 10^{-16}$).

COMPARISON OF SYMPATRIC SPECIES IN THE TEMPERATE BIOME

The mean body size of the generalist (*P. amentata*) was 2.63 ± 0.15 mm ($n = 65$), while the mean body size of the specialist (*P. agricola*) was 2.19 ± 0.13 mm ($n = 68$). There was an effect of species and a positive effect of female body size on clutch size (Table 2, Fig. 1B). This effect of body size on clutch size was the same for the two species, which means that contrary to the situation in the Arctic, both specialist and generalist species increased clutch size with increasing body size at the same rate (63.17, Fig. 1B). Mean clutch size in *P. amentata* and *P. agricola* was 56 ± 16 ($n = 65$) and 46 ± 11 ($n = 68$), respectively and was significantly higher in *P. amentata* (one-tailed *t*-test, $t = -4.23$, d.f. $= 115.57$, $P = 2.32 \times 10^{-5}$). Our results only showed an effect of species on mean egg volume, but no effect of body size was detected (Table 2). Mean egg volume in *P. amentata* and *P. agricola* was 0.44 ± 0.07 mm^3 ($n = 31$) and 0.35 ± 0.05 mm^3 ($n = 46$), respectively and was significantly higher in *P. amentata* (one-tailed *t*-test, $t = -6.44$, d.f. $= 71.29$, $P = 5.94 \times 10^{-9}$). There was a positive effect of female body size on the mean size of the postembryonic individuals, and this effect was the same for both species (Table 2, Supporting Information Fig. S1). Mean size of the postembryonic individuals was 0.54 ± 0.04 mm ($n = 34$) and 0.49 ± 0.05 mm ($n = 22$) for *P. amentata* and *P. agricola*, respectively and was significantly higher in *P. amentata* (one-tailed *t*-test, $t = 3.98$, d.f. $= 54$, $P = 0.00010$).

DISCUSSION

In this study, we assessed the combined effects of environmental constraints and habitat specialization on reproductive output in wolf spider species (Lycosidae). We had three hypotheses: (1) fecundity should increase with female body size while egg quality would vary independently, (2) specialist species should invest more in fecundity than generalist species and (3)

Table 2. ANCOVA analyses details of the effect of body size on reproductive output. Values are given for final models

|	Initial model	Response variable	F	d.f.	R^2	P	Explanatory variables	F	P
In Kobbefjord at sea level: effect of body size on reproductive traits, sympatry of *P. hyperborea* and *P. furcifera*	Clutch size ~ species*body size	Clutch size	219.40	115	0.85	**< 2.2.10^{-16}**	Species	9.45	**0.0026**
							Body size	56.83	**1.19×10^{-11}**
							Species: body size	7.43	**0.0074**
	Mean egg volume ~ species*body size	Mean egg volume	270.6	117	0.70	**<2.2.10^{-16}**	Species	270.56	**5.44×10^{-7}**
In Belgium-the Netherlands at sea level: effect of body size on reproductive traits, sympatry of *P. amentata* and *P. agricola*	Clutch size ~ species*body size	Clutch size	57.09	130	0.46	**<2.2.10^{-16}**	Species	24.01	**2.80×10^{-06}**
							Body size	84.41	**8.26×10^{-16}**
	Mean egg volume ~ species*body size	Mean egg volume	43.15	85	0.33	**3.85×10^{-09}**	Species	43.15	**3.85×10^{-09}**
	Mean baby size ~ species*body size	Mean baby size	19.88	45	0.29	**5.44×10^{-05}**	Body size	19.88	**5.44×10^{-05}**

Significant *P*-values are highlighted in bold.
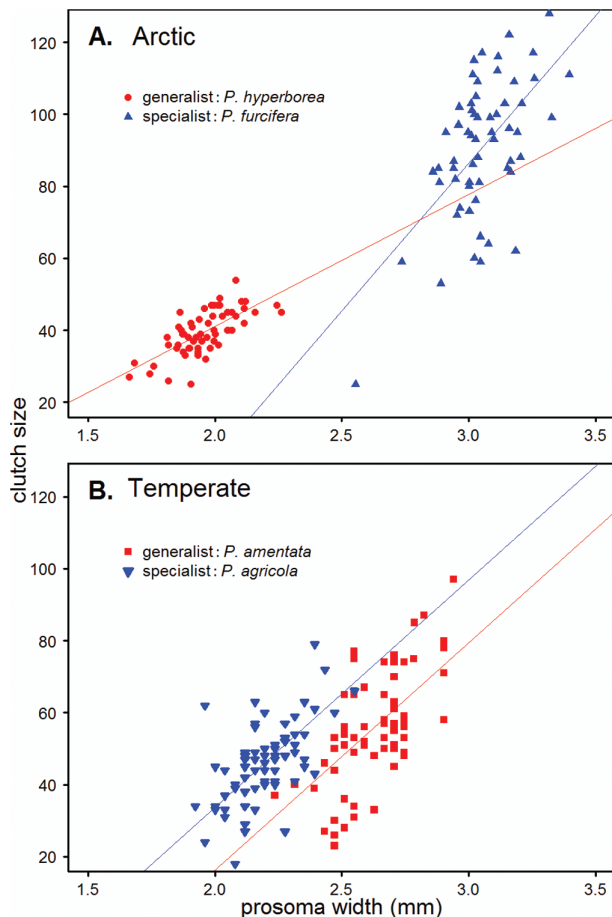
Figure 1. Clutch size depending on female body size. (A) In the Arctic. *P. hyperborea* (LLSR, clutch size = −32.19 + 36.63*prosoma width, $F = 56.11$, 58 d.f., $R^2 = 0.48$, $P = 4.4 \times 10^{-10}$), *P. furcifera* (LLSR, clutch size = −159.28 + 81.93*prosoma width, $F = 30.49$, 57 d.f., $R^2 = 0.34$, $P = 8.6 \times 10^{-7}$). (B) In a temperate habitat. ANCOVA, clutch size = −92.70 (−17.42 for *P. amentata*) + 63.17*prosoma width, $F = 57.09$, 130 d.f., $R^2 = 0.46$, $P < 2.2 \times 10^{-16}$.

reproductive trade-offs are expected to be stronger in the Arctic where the conditions are harsher. We found that larger females produced more offspring independently of species or location. We also found that specialist species invested more in clutch size than did generalist species. Moreover, our results indicate that, in the Arctic, species developed distinct strategies likely in order not to overlap each other's ecological niches as a consequence of limited food resources, contrary to temperate species which presented similar reproductive strategies.

ADVANTAGE OF A LARGER BODY SIZE

In accordance with our first hypothesis, independently of species or location, fecundity (clutch size) increased with body size while egg quality (egg volume) varied independently of female body size. For temperate species, postembryonic size, but not egg volume, increased with female body size and we discuss this result in the third part of the discussion. These results are coherent with other findings in wolf spiders where fecundity, but not egg quality, increased with body size (Simpson, 1993; Pétillon *et al.*, 2009; Puzin *et al.*, 2011). Indeed, egg quality appears to be better explained by body condition (Bowden & Buddle, 2012a). These studies showed that having a larger body size is an advantage for the female which may consequently increase her fecundity, and also often offspring quality (Marshall & Gittleman, 1994). One experimental approach to test this hypothesis on a functional basis would be to impose dietary restriction on the females (Adler *et al.*, 2013) or to manipulate their energy storage (Cox, Lovern & Calsbeek, 2014). Last, we know that the adult body size and reproductive output of Arctic wolf spiders may fluctuate according to snowmelt timing, and this occurs in space and time (Høye *et al.*, 2009; Bowden *et al.*, 2015), creating differing activity periods in which to obtain resources. Hence, we cannot completely discount the possibility that the timing of specimen collection (i.e. different years) could influence our results. We do, however, presume the effect size to be greater than the year of collection and, ultimately, that the same pattern would hold as with other biogeographical phenomena (e.g. Ernst & Buddle, 2015).

BETTER ADAPTATION OF SPECIALISTS TO THEIR ENVIRONMENT

In the Arctic, clutch size of the specialist *P. furcifera* increased with body size at a higher rate than the generalist *P. hyperborea* (Fig. 1A); whereas in the temperate habitat, clutch size of both species increased with body size at the same rate but the specialist *P. agricola* invested more in clutch size for the same body size (Fig. 1B). This confirms our second hypothesis that specialist species are better adapted to their environment and are therefore able to invest more into fecundity (cf. Pétillon *et al.*, 2009).

Two main differences between the Arctic species are striking when observing body size and niche specialization. Indeed, the specialist species *P. furcifera* was, on average, 1.6 times larger than the generalist species *P. hyperborea*. Consequently, *P. furcifera* is able to increase its fecundity more efficiently than *P. hyperborea*. This result suggests that *P. furcifera* may occupy a habitat of better fit, given its niche requirements. However, while *P. furcifera* might be better adapted to its environment as a habitat specialist, our findings could also be due to the fact that larger individuals are able to invest more energy in fecundity and quality

of progeny (Marshall & Gittleman, 1994). These ideas about differences in life history investments between specialists and generalists should be further investigated using other species and groups, particularly to gain a better understanding of the relation between body size and reproductive output. In the temperate habitat, and contrary to the previous case, the specialist species was significantly smaller. Indeed, on average, body size of *P. agricola* was 1.2 times smaller than *P. amentata*. Consequently, this finding adds support to the specialist adaptation hypothesis. Such an adaptation could be linked to physical constraints (Lambeets, Maelfait & Bonte, 2008), to feeding specialization (Roslin & Salminen, 2008) or to physiological constraints (Pétillon *et al.*, 2011). These two species were, however, collected in a riparian environment where the temperature variability is high and the river is prone to unpredictable inundation during the reproductive season (Lambeets *et al.*, 2008). We hence hypothesize that adaptation of the specialist is mainly linked to physical constraints, namely rapid changes in water level and temperature.

HIGHER COMPETITION IN THE ARCTIC

We found that the specialist and the generalist species in the temperate habitat adopted similar strategies, while the Arctic species did not. This could be related to the relatively harsher climatic conditions of the Arctic, which may ultimately result in resource limitation. Intraguild predation, a unique variety of competition common in spiders, is believed to be a foraging strategy that helps overcome the effects of limited resources (Wise, 2006). It has been shown in *P. palustris*, for example, that cannibalism increased as a consequence of food limitation (Rickers & Scheu, 2005). Further experimentation could compare this phenomenon among niche specializations and habitats. We propose that in the Arctic, the relative simplicity of the environment would also increase inter-specific competition, due to a limited number of ecological niches, leading to niche overlap. In our case, the lack of alternative food resources and the adaptation of the specialist species to local conditions could be synergic factors leading to inter-specific competition, potentially reflected by differential resource acquisition, differential female fecundity and differential search ability (Reitz & Trumble, 2002).

The size of postembryonic individuals increased significantly with female body size in both of the temperate species, but the volume of the eggs did not in the Arctic species. As mentioned above, the riparian environment of the temperate species also presents harsh conditions due to irregular flooding and extreme temperatures but it is extremely prey-rich (e.g. for lycosids: Paetzold, Schubert & Tockner, 2005), which suggests that food is not a limiting factor in the temperate environment. Hence, both temperate species were even able to increase simultaneously quantity and quality of offspring, which supports our third hypothesis of a non-food-limited habitat.

In addition, as stated in the introduction, we must keep in mind that temperate species might produce more than one clutch per lifetime. However, given the relatively narrow window of collection at each locality, it is unlikely that second clutches were collected in high enough frequency to significantly influence the variation in our data. Total reproductive output is hard to assess on relatively small spider species given that individual tracking is almost impossible. Moreover, in our case, data acquisition requires field collected females, hence totally impeding individual tracking. We advocate for further investigation of the additive or multiplicative effects that habitat specialization and elevation/latitude play in driving life history variation. Moreover, laboratory based experiments would help elucidate the relative roles of plasticity and adaptation in these patterns. We conclude that habitat specialization as well as the environment can have significant impacts on reproductive investment between congeneric species.

SHARED DATA

Data available from the Dryad Digital Repository: Amelin *et al.*, (2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Sampling details of hand collections of *Pardosa* species. All collections were done at sea level.
Figure S1. Postembryonic size depending on female size in a temperate habitat. ANCOVA, postembryonic individual size = 0.26 + 0.10*prosoma width, F = 19.88, 45 d.f., R^2 = 0.29, P = 5.4 × 10^{-5}.