Elevational Variation of Reproductive Traits in Five Pardosa (Lycosidae) Species

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Elevational variation of reproductive traits in five *Pardosa* (Lycosidae) species

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Abstract

Differentiations in reproductive traits along climatic gradients can be substantial for a species to spread along a wide spatial range. We compared the reproductive effort allocated to first egg sacs of five species of the genus *Pardosa: P. palustris* (Linnaeus 1758), *P. amentata* (Clerck 1757), *P. lugubris* (Walckenaer 1802), *P. hyperborea* (Thorell 1872), and *P. riparia* (C. L. Koch 1833) along three elevation transects in central Norway. We tested whether population differences are consistent among the three transects, respectively along the elevational gradient. We assumed that the harsh environments of alpine areas would lead to adaptations in reproductive traits resulting in larger eggs but smaller clutches at higher elevations. The results show that female size and egg number were positively correlated among all species. However, no clear elevation-related trend was found. Other traits did not change consistently between species and along the elevational gradient. We assume that local microclimatic impacts on spider fitness are a crucial but poorly understood factor. Without further knowledge about adaptation and phenotypic plasticity in ectotherms, modeling of possible future reproduction biology might remain flawed.

Introduction

Many ectotherm species that are widely distributed along elevation and latitudinal gradients have to cope with extreme differences in environmental conditions, in particular at the upper and lower boundaries of their distribution (e.g., Hodkinson, 2005). Species adaptation (e.g., in reproductive traits) along elevation gradients provide help in understanding how species or populations may react to environmental changes (Hodkinson, 2005). Reproductive traits can vary between species, between populations of a certain species, and between individuals of a population (e.g., Fox and Czesak, 2000; Fischer et al., 2002; Moya-Laraño, 2002; Høye and Hammel, 2010). Variations in reproductive traits are controlled by a number of factors that include maternal fitness and environmental conditions (Simpson, 1995; Hendrickx and Maelfait, 2003). However, environmental factors such as temperature and food supply can also interact with intrinsic factors like maternal size (Azevedo et al., 1996; Bauerfeind and Fischer, 2008). The influence of these factors on traits such as egg size is not completely understood so far (Bernardo, 1996; Fox and Czesak, 2000).

One of the primary challenges for ecologists today is to assess the ecological impact of global environmental changes on physiological traits in different geographic areas (Bozinovic et al., 2011). Comparative studies of species ecology along different elevational and latitudinal gradients may provide important information on the response of populations or communities to climatic change at any point in time (Hodkinson, 2005). In particular, research along elevational gradient and the related environmental changes might deliver important findings in how species react to changing climatic conditions. Körner (2007) identified four main climatic factors that change along an elevational gradient and that are relevant for organisms: (a) decrease in atmospheric pressure, (b) reduction of atmospheric temperature, (c) increasing radiation under a cloudless sky, and (d) a higher fraction of ultraviolet-B (UV-B) radiation. Other climatic factors are not considered relevant for unidirectional trends with elevation. Evolutionary theory suggests that harsher environments (e.g., alpine areas) can lead to a trade-off between separate life history traits (Hendrickx et al., 2003; Norry et al., 2006). For several invertebrates, it has been shown that fitness-related traits, including characteristics of life cycle and reproduction, can vary along latitudinal and along elevation climatic gradients (David and Bocquet, 1975; Berven and Gill, 1983; Dingle et al., 1990; Ayres and Scriber, 1994; Tatar et al., 1997; Telfer and Hassall, 1999; Lencioni, 2004; Hodkinson, 2005; Samietz et al., 2005).

Lycosid spiders (i.e., wolf spiders) are well-suited model organisms for various aspects of (spider) ecology, including the influence of environmental conditions on spiders (see, e.g., Hendrickx and Maelfait, 2003; Löffler and Finch, 2005; Høye et al., 2009; Høye and Hammel, 2010), because they colonize a huge variety of terrestrial habitats from sea level to high alpine areas. Thus, wolf spiders have become the most intensively studied spider family to date (Wise, 1993, 2006). For studies on reproductive traits, wolf spiders are exceptionally suitable model organisms, as females carry their eggs in a sac attached to the spinnerets. This makes it possible to relate reproductive traits (e.g., egg number, egg size) to each individual female. In this study we analyzed traits of lycosid spiders of the genus *Pardosa* as well as the influence of elevation on these traits. Since lycosid spiders are one of the main predators in alpine environments (Wise, 1993) we aimed to test whether climatic gradients related to elevation are driving forces for adaptation in these species.

During a single reproductive period, at lower altitudes, each female spider produces up to three egg sacs, which differ in clutch and egg size. In alpine areas usually only two egg sacs are produced (e.g., Edgar, 1971a; Kessler, 1971; Steigen, 1975; Bayram, 2000; Hendrickx and Maelfait, 2003). On a micro-spatial scale, Frick et al. (2007a) found no differences in temperature preference between females with and without egg sacs. This at least indicates that females do not actively search for higher local temperatures to increase the speed of egg development. However, the duration of egg sac carrying varies with temperature (Schmoller, 1970; Steigen, 1975), and the detailed characteristics of reproductive clines in wolf spiders along a thermal gradient remain unclear.

We expected elevation-dependent differences and adaptations in the reproduction traits of wolf spiders: bigger eggs but smaller clutches may occur at higher elevations, forced by the harsher environmental conditions at higher altitudes. This assumption is in line with the life history theory (Sibly and Calow, 1986; Simpson, 1995; Tanaka, 1995; Tamate and Maekawa, 2000).

Material and Methods

STUDY AREA

Three transects along elevational gradients on three different mountains (Blåhø, Svarthovda, and Gråsida) were studied in the research regions Vågå and Dovre (Oppland). The study areas were located in the central southern and most continental part of Norway (Moen, 1998) at about 62°N and 9°E (Fig. 1). For a detailed description of the study areas, see, for example, Löffler (2002). The alpine environment begins above the tree line, which is situated at around 1000–1050 m a.s.l., with a transition zone between the low alpine and middle alpine belt at about 1350 m a.s.l. The vegetation in the low-alpine belt is dominated by shrub and heath communities, whereas the middle-alpine belt is dominated by graminoids (Dahl, 1986).

At Mount Blåhø, the elevation transect reached from 360 m to 1610 m a.s.l. and included nine sampling sites below and eight above the tree line. At Gråsida, the elevation transect covers a range from 470 m to 1440 m a.s.l., with eight sampling sites falling below and eight sites above the tree line. The transect at Svarthovda ranged from 610 m to 1390 m a.s.l. Here, the tree line was situated at around 900 m a.s.l. Six sites were established below and six above the tree line.

SAMPLING OF TRAITS

Sampling sites were chosen for their elevation range and typical aspects of lycosid preferred habitats (Lomnicki, 1963; Otto and Svensson, 1982; Frick et al., 2007b). Pre-examinations were implemented to assess if lycosid spiders were present. The elevation distance between the sampling sites was around 60–70 m. Each sampling site was representative in its floristic composition and vegetation structure. The size of each sampling site was approximately 100 m².

In this study, we focused on the traits prosoma width, egg number, and egg size. Prosoma width is a powerful trait for determining the different development stages and the fitness of lycosid females (Hagstrum, 1971; Edgar, 1971a, 1971b; Marshall and Gittleman, 1994; Pickavance, 2001; Hendrickx and Maelfait, 2003). Egg number is commonly closely related to female size, since a bigger female profits by the augmented egg production (Vertainen et al., 2000). Egg size is a good proxy for reproduction effort, because bigger eggs result in bigger, healthier offspring with, for example, a higher starvation resistance (Edgar, 1971a; Tanaka, 1995; Fox and Czesak, 2000).

In order to sample these traits, female wolf spiders carrying egg sacs were hand-collected from the three transects between 24 May and 26 July 2006, on warm, sunny days, when wolf spiders of the genus *Pardosa* are most active (Steigen, 1975; Buddle, 2000). Each site within each transect was sampled several times for about one hour by one person. Because of the high number of sampling sites, the three transects were divided into two sections at the tree line. Sites below the tree line were sampled on one day, sites above the tree line on the consecutive day of the sampling period. In order to avoid time-of-day related artifacts in the sampling, we varied the spatial pattern of sampling, for example, starting at the top-most site conducting the sampling downward alternating with the lowest situated site upward. As soon as the sampling sites became snow-free, they were monitored constantly at least once a week until the first females with egg sacs could be sampled. Kessler (1971) stated that lycosids usually carry their egg sac in a six-week period from May until the end of June with each single female carrying the sac for not more than one or two weeks. This timing and the fact that second egg sacs contain only 50%–60% of the number of eggs compared with first egg sacs (Kessler, 1971) allowed us the identification and removal of second egg sacs from our sample. Second egg sacs
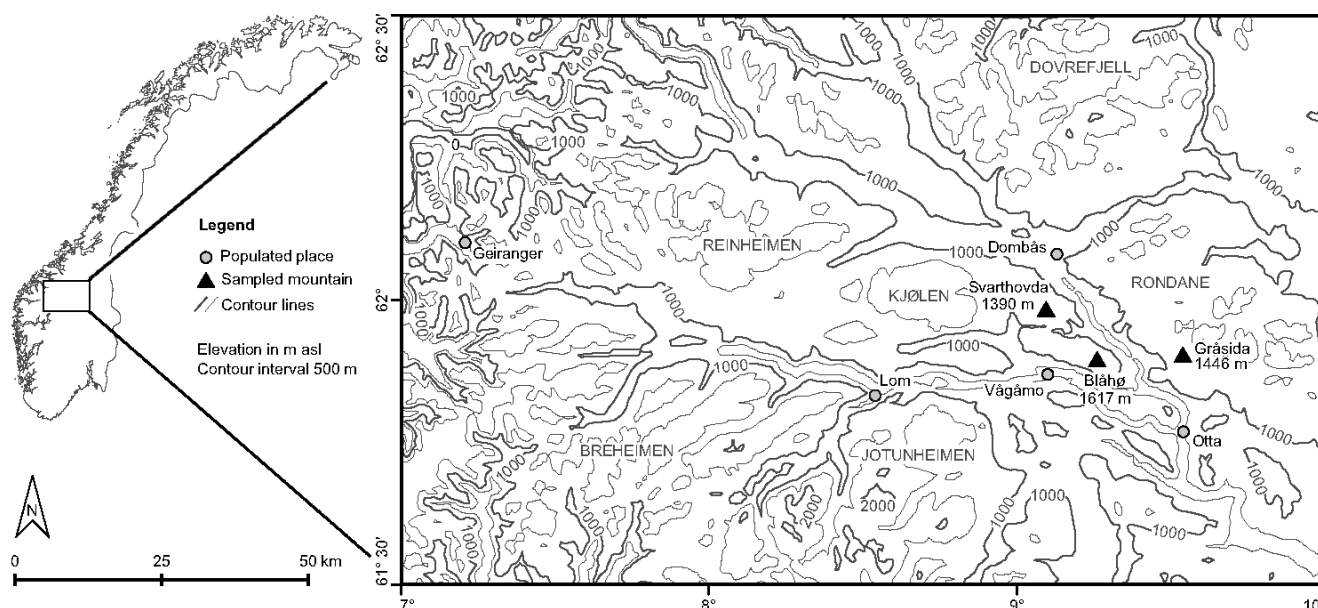

FIGURE 1. Map of the research area in southern central Norway with focus on three mountain tops: Blåhø, Gråsida, and Svarthovda.

were assumed to contribute to the recruitment of the population to a much lesser extent than first egg sacs (Steigen, 1975). Every female was held separately to avoid cannibalism and exchange of egg sacs. Female lycosids and egg sacs were preserved in 70% ethanol for at least four weeks to make sure that the eggshell was able to extend to its maximum volume (Hendrickx and Maelfait, 2003). Egg number was determined by counting the eggs and juveniles in the egg sac, assuming that all eggs in an egg sac would develop (Hackmann, 1957; Edgar, 1971a). We identified spiders following Almquist (2005). All collections were stored at the Department for Geography at the University of Bonn, Germany. We took digital photographs of all females and of 10 eggs from each female with a Nikon photo-ocular and a 100× digital magnification. From these photographs, we measured female prosoma width as well as egg length and width to the nearest 0.01 mm using the software "Bild'o'meter" (2006, Version 1.0.3, Münster, for further information contact M. Mühlen at matthias@muehlen.info). Only species-specific results were used, as patterns found at an interspecific level (i.e., within a pooled analysis of all species of wolf spiders) may not hold true for a single species. Based on the measured egg length (EL) and egg width (EW) we calculated egg size (EV) following Hendrickx et al. (2003, equation 1):

$$EV = \frac{\pi}{6} \; x \; EL \; x \; EW^2. \qquad (1)$$

STATISTICAL ANALYSIS

The sampled data on prosoma width, egg size, and egg number were subjected to a Principal Component Analysis (PCA, Hotelling, 1933). Prior to this analysis, the data were tested for Gaussian distribution and transformed, if necessary. PCA allows us to reduce the dimensionality of the trait space and to identify, quantify, and illustrate collinearities between the traits. The principal components (PCs), that is, the axes of the PCA space, represent the original variation of the data in hierarchically decreasing order. The percentage of the original variation that is represented by each axis is described as explained variance (ExV). A separate PCA was used for each site and species to analyze interspecific and intersite differences in the relation of the traits and elevation. For interpretation purposes and in order to analyze the relation between the three traits, we projected the traits as vectors into the PCA space. The direction of the vectors with respect to the PCs indicates the correlation with the respective axes; the length of the vector illustrates the strength of this correlation. For the trait data, these vectors thus correspond to their loadings on the axes. More important, however, is the similarity of the direction of two trait-vectors that describes the degree of intercorrelation between these traits. Further, covariables such as elevation in this study can be projected and analyzed in the PCA space. This allows us to draw conclusions on possible relations between trait distributions and environmental parameters. We used permutation tests with 999 permutations of the variables to evaluate the significance of the relations between the PCs, traits, and elevation. In the present study, we use the PCA mainly as a visualization method to analyze the intercorrelation of traits and their relation to the elevation gradient. A thorough analysis of the loadings or interpretation of the principal components is not required to answer the research question. Although the traits were analyzed for all occurring species, the PCA was only used to analyze species-specific data with an appropriate sample size of individuals with first egg sacs containing eggs.
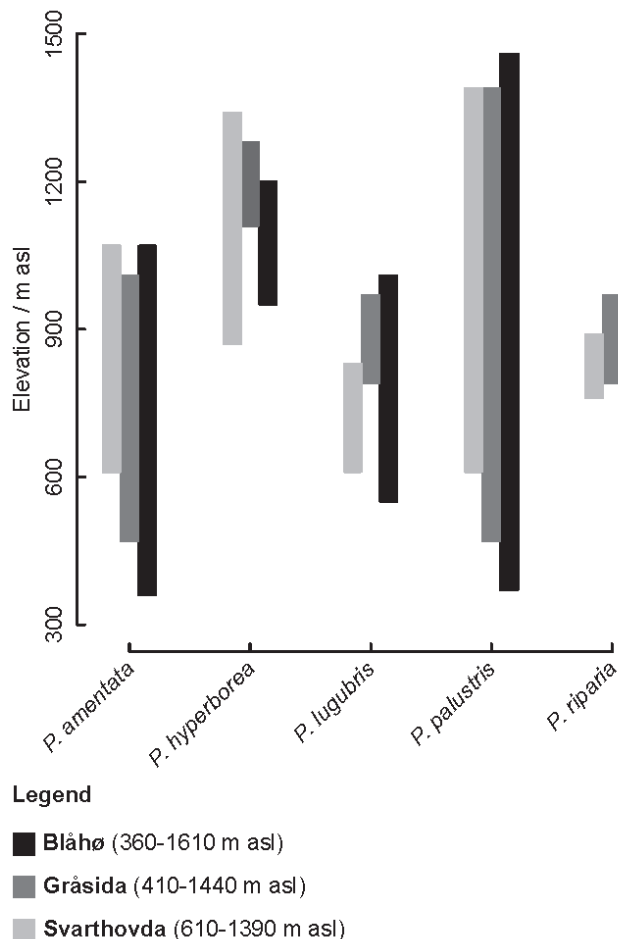
Results

A total of 1558 female lycosids with egg sacs of 13 species were sampled along the three transects (44 sampling sites). An overview of the sample and the variation of the measured traits for the five *Pardosa* species in focus is given in Table 1. Individuals of *P. amentata*, *P. lugubris*, and *P. riparia* were only found up to the transition zone between the tree line and the alpine area. Individuals of *P. hyperborea* were only found at alpine sites and in the transition zone, while individuals of *P. palustris* were collected almost along the entire elevation gradient at sites below and above the tree line (Fig. 2).

The PCA for the five *Pardosa* species show a strong correlation between prosoma width and egg number (Fig. 3). This correlation is, however, the only feature that is generally applicable for the five spe-

TABLE 1

Morphometric and reproductive traits for the 5 lycosid species sampled at the 44 sampling sites (EN = egg number, PW = prosoma width in mm, EV = egg volume in mm³, ER = elevation range, *only first egg sacs).

Species	*n*	EN*	Egg volume Ø*	EV Ø range*	PW (mm)	PW range (mm)	ER m a.s.l.	First sampled (date/elevation m a.s.l.)
Pardosa amentata (Clerck, 1757)	237	54.5 ± 11.53 (*n* = 218)	0.40 ± 0.045 (*n* = 1750)	0.28–0.55	2.51 ± 0.17	2.04–2.92	360–1070	24 May 2006/360 m
Pardosa lugubris (Walckenaer, 1802)	220	37.72 ± 6.37 (*n* = 204)	0.37 ± 0.038 (*n* = 1500)	0.29–0.50	2.12 ± 0.13	1.65–2.49	550–1010	12 June 2006/580 m
Pardosa palustris (Linnaeus, 1758)	747	45.67 ± 11.43 (*n* = 712)	0.36 ± 0.044 (*n* = 3630)	0.25–0.59	2.21 ± 0.15 (*n* = 741)	1.76–2.70	370–1460	15 June 2006/1010 m
Pardosa riparia (C.L. Koch, 1833)	125	37.54 ± 6.46 (*n* = 120)	0.34 ± 0.036 (*n* = 950)	0.24–0.43	2.04 ± 0.13	1.77–2.39	760–1010	15 June 2006/970 m
Pardosa hyperborea (Thorell, 1872)	127	32.07 ± 6.85 (*n* = 121)	0.32 ± 0.037 (*n* = 720)	0.25–0.41	1.84 ± 0.15 (*n* = 126)	1.48–2.60	870–1340	23 June 2006/890 m

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Discussion

Reproductive traits in lycosid wolf spiders along elevation gradients, with a focus on *Pardosa,* differed between the different species of *Pardosa*. Our assumption, that under harsh environmental conditions at higher elevation species of the genus *Pardosa* would tend to produce bigger eggs but smaller egg number, was not confirmed. However, egg numbers were positively correlated with female size, both inter- and intra-specifically along the three elevation gradients. This relationship is in line with general rules of invertebrate ecology, including wolf spiders, other spider families (Leather, 1988; Roff, 1992; Stearns, 1992; Kessler, 1971; Brown et al., 2003), and some holometabolous insects such as butterflies (Tammaru et al., 1996, 2002; Bauerfeind and Fischer, 2008), emphasizing that a bigger size in female spiders is beneficial due to the augmented egg production (Vertainen et al., 2000).

In general, alpine environments are associated with hazard-prone environments regarding the severity of environmental conditions, strong seasonality, snow cover, fine-scale spatio-temporal variability and problems modeling or predicting these conditions (e.g., Franz, 1979; Otto and Svensson, 1982; Lencioni, 2004; Nagy and Grabherr, 2009; Wundram et al., 2010; Hein et al., 2014a). In accordance with life history theory, several studies showed that under extreme environmental conditions smaller clutches with bigger eggs should be produced (Sibly and Calow, 1986; Simpson, 1995; Tanaka, 1995; Tamate and Maekawa, 2000; Hendrickx and Maelfait, 2003). Both traits have been assumed to compete for limited maternal resources, resulting in the phenotypic trade-off of "bigger but less" (Smith and Fretwell, 1974; Bauerfeind and Fischer, 2008). Bigger offspring develop faster and thus mature earlier, which is assumed to be favorable in harsh environments (Fox and Czesak, 2000). However, our results did not show a general coherence between high elevations and an adaptation in reproduction traits of the five *Pardosa* species in focus. Thus female size seems to explain most of the variation in reproduction in the different species. Theoretically, inter-relationships between offspring size and female size are expected to influence both offspring and parental fitness (Clutton-Brock, 1991; Marshall and Gittleman, 1994; Bernardo, 1996). However, earlier studies concerning wolf spiders had not found correlations between female size and egg or offspring size (Kessler, 1971; Brown et al., 2003; Hendrickx and Maelfait, 2003). This has been assumed to be a result of the strong food limitation in many species. Females are unable to produce normal or larger sized eggs or offspring because of this limitation (Wise, 1993, 2006; Brown et al., 2003). Other selective pressures such as feeding patterns, parent-offspring conflict, and environmental conditions, may be important constraints on egg size as well (Parker and Begon, 1986; Klingenberg and Spence, 1997). To gain further information on the essence of elevation-related effects, additional, comparable studies should be provided (Körner, 2007). In this context, the focus should also be on factors that are not closely related to elevation, like habitat type, competition, and prey availability (e.g., Buddle, 2000; Hendrickx and Maelfait, 2003; Høye et al., 2009; Öberg, 2009).

Høye et al. (2009) and Høye and Hammel (2010) showed that wolf spiders in a harsh arctic environment profit from longer seasons, resulting in a larger body size, with unpredictable impacts on future community structure. Our results show that general conclusions on elevation-dependent effects on prosoma width and reproductive traits are difficult to state. Even though we found a decrease in prosoma width in *P. palustris* at Gråsida and Svarthovda, for Blåhø we did not. Blåhø seems to be somehow different com-

FIGURE 2. **Elevation ranges of the five *Pardosa* species sampled along the three gradients.** *Pardosa amentata*, *P. lugubris,* and *P. riparia* **are found up to the tree line at the three transects, while** *P. hyperborea* **was found only above and in the transition zone between tree line and the alpine. The only species occurring along almost the entire elevation gradients was** *P. palustris.*
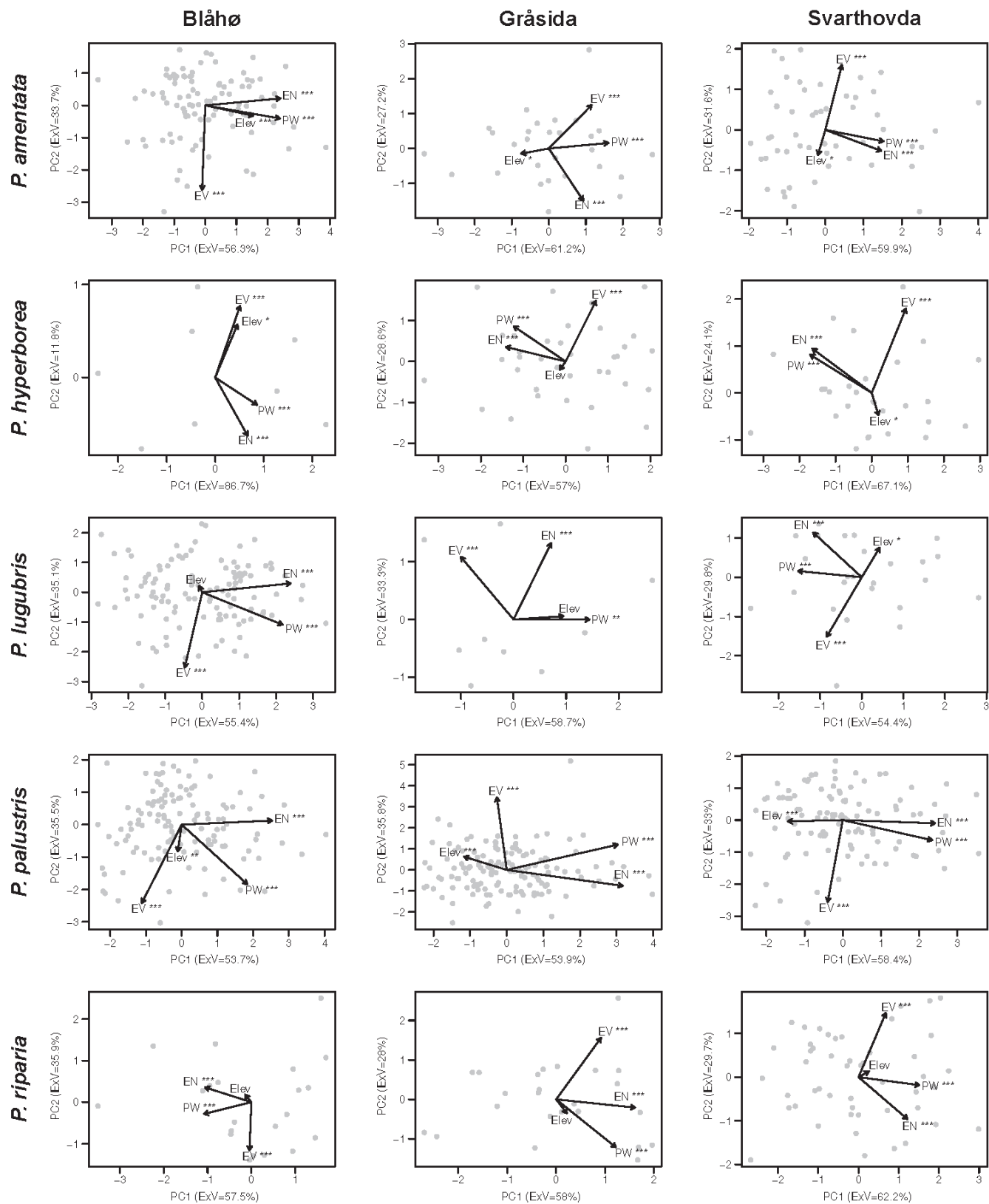
cies at the three locations. Moreover, we found partially diverging and even contradictory species-specific trends for some of the traits that were analyzed. On the one hand, *P. amentata* at Blåhø showed an increased prosoma width and thus a greater number of eggs at higher elevations, on the other hand the results at Gråsida indicated a decrease in prosoma width at higher elevations; egg number remained unaffected here. For *P. hyperborea, P. lugubris,* and *P. riparia* no clear elevation-related trend in egg number or prosoma width emerged. *Pardosa palustris,* the species with the widest elevational range in our study, displayed a strong decrease in prosoma width at Gråsida and Svarthovda at higher elevations, while at Blåhø this effect was not observed at all. Elevation-dependent constraints on egg size were only visible along some of the gradients. For *P. amentata* at Svarthovda, egg size decreased at higher elevations. For *P. hyperborea,* egg size increased with increasing elevation at Blåhø, while at Svarthovda the opposite effect was visible. For *P. lugubris,* a decrease in egg size at higher elevations was observed at Svarthovda. For *P. palustris,* egg size increased at higher elevation at Blåhø. Along the other gradients we could not find any relationship between egg size and elevation. Along none of the transects could relations between decreasing egg number and increasing egg size or vice versa be observed.

FIGURE 3. Principal Component Analysis (PCA) for the five *Pardosa* species along the three elevation gradients. The axes of the PCA space represent the original variation of the data in hierarchically decreasing order; their information content is expressed as explained variance (ExV). The direction of the vectors with respect to the PCs indicates the correlation with the respective axes; the length of the vector illustrates the strength of this correlation. The significance of the correlations is indicated by asterisks. Elev = elevation a.s.l.; Egg # = egg number; ES = egg size; PW = prosoma width.

pared to the two other transects; unfortunately, we cannot provide a sufficient explanation for that, yet.

Findings on spatial patterns of spider size obviously cannot be generalized without caution, since elevation-related effects may be overlain by microclimatic site conditions. Legault and Weis (2013) found an increased body mass due to artificially increased snow cover in *Pardosa lapponica* in a subarctic tundra heath landscape, within a single year period. Scherrer and Körner (2011) showed that microclimatic site conditions might buffer the effects of increasing temperatures in alpine environments. Pape et al. (2009) showed the difficulties of modeling climatic conditions at specific alpine sites, where microclimatic conditions are inadequately known. As we found no consistent trends along elevational gradients, we suggest future research to set stronger focus on the influence of microclimate, behavioral adaptation, and competition on physiological traits of alpine wolf spiders. This will be necessary to fill the gap in understanding reproductive traits of lycosid wolf spiders, and supply findings on the relation between a species physiology and its distribution. Consequently, these results raise new questions about adaptation strategies in female spiders to alpine environments. A more widespread species like *P. palustris* obviously copes with the alpine environmental conditions in a more sufficient way and has a higher phenotypic plasticity than other spiders of the genus *Pardosa*. An extensive phenotypic plasticity is assumed to be the reason why a certain species will persist in changing environments (Scharf et al., 2010). The knowledge of phenotypic plasticity in a certain species is imperative to gain information about the structure and assemblages of future ecosystems (e.g., Hein et al., 2014b). We showed that adaptation strategies in closely related species can be varied even at local scales.

Acknowledgments

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