



Egg size versus egg number trade-off in the alpine-tundra wolf spider, *Pardosa palustris* (Araneae: Lycosidae)

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Abstract

The effect of environmental conditions on reproductive traits in spiders is not completely understood. We studied the trade-off between the egg number and egg size of a common spider species along an elevational gradient in Norway. Life history theory predicts that egg size should decrease and clutch size increase as temperatures rise. In 2006, 2010, and 2014, female lycosid spiders (*Pardosa palustris*) carrying first egg sacs were hand sampled from 690 to 1460 m above sea level (a.s.l.). The eggs were counted, and the body and egg sizes for each female were individually estimated using digital photography. An analysis of covariance was performed using linear mixed-effects models to test for trade-off differences between sampling years, and along the elevational gradient. Unexpectedly, the egg size versus number trade-off was consistent along the elevational gradient, and thus appeared to be independent of elevation-induced temperature changes. However, this trade-off varied considerably between years. Egg-size variations in relation to body size appeared to be independent of year and did not vary along the elevational gradient. Our results revealed that the trade-off between egg number and egg size does not always hold and might be more plastic than assumed. This suggests that *P. palustris*, which has a broad habitat niche and a wide geographic distribution, will easily cope with temperature-regime shifts in cold environments. Consequently, this might lead to advantages regarding the offspring survival rate relative to coexisting species, and thus to changes in the terrestrial arthropod community of alpine-tundra ecosystems.

Keywords Offspring · Elevation · Trade-off · Temperature rise · Norway

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Introduction

Ectothermic species often live below their optimal temperature range in cold environments, especially in terms of development and reproduction, during the relatively short summer season (Danks 1999, 2004). Thus, ectotherms show specific adaptation strategies to cope with these critical conditions. Consequently, even small increases in temperature towards their optimal temperature range in these environments foster a wide range of physiological processes in these species (Willmer et al. 2005). Progressive climate change with its higher temperatures and increased season length is expected to affect the reproductive success of ectothermic species (Høye et al. 2009; Pike 2014). Previous studies have shown how increases in temperature and season length affect individual species directly through alterations in body size (Gardner et al. 2011; Bowden et al. 2015), as well as indirectly by altering their biotic interactions (Zarnetske et al. 2012; Post 2013). Thus, one major aspect of ecological research should be to

study the effect of temperature on the reproductive traits of species in their natural environments (Kessler 1971; Rickers and Scheu 2005). Environmental temperature is extremely important for the metabolic rate of spiders, and it controls various traits such as food utilization and egg production (Palanichamy 1985; Schmalhofer 2011; Iida et al. 2016). Lycosid spiders are considered a suitable model organism for assessing the changes in reproductive success induced by climate change for several reasons. First, lycosid spiders are speciose and occur in high abundance, even in relatively cold environments (Bowden and Buddle 2010; Finch and Löffler 2010; Visakorpi et al. 2015). Second, they are known to be highly sensitive, especially reproductively (Hendrickx et al. 2003) or in terms of body size (Legault and Weis 2013; Puzin et al. 2014), to changing environmental conditions on various spatial scales. Third, female lycosidae are of particular interest because they carry their eggs in a sac attached to their spinnerets, which allows clutch and egg size to be assigned to specific individuals.

In cold environments such as alpine-tundra ecosystems, temperatures below 0 °C become critical for the spiders because sub-zero temperatures can cause fatal damage to the organism, slowing its metabolic rate and locomotor capabilities (Kirchner 1987; Danks 2004). Previous studies have shown that lycosid females tend to produce larger eggs under harsh environmental conditions, which increases offspring fitness (Hendrickx et al. 2003; Walker et al. 2003; Pétilon et al. 2009). In these circumstances, life history theory predicts a smaller but higher number of eggs in response to increasing temperatures (Blanckenhorn 2000; Fox and Czesak 2000). This has been assumed to be a consequence of the well-described trade-off between clutch size and egg size in ectothermic species in response to environmental conditions (Smith and Fretwell 1974; Parker and Begon 1986).

However, our knowledge of how temperature variations, both elevation-induced and inter-annual changes, control spider fitness and reproduction in ectotherms in the field is still limited (e.g. Bernardo 1996; Berger et al. 2008; Stahlschmidt and Adamo 2015). In our study, we assessed various reproductive and fitness proxies such as egg size, clutch size, and prosoma width of the mother spider along an elevational gradient and in three sampling years. We tested for (a) a trade-off between clutch size and egg volume; (b) a relationship between body size (prosoma width) and egg volume; and (c) a relationship between prosoma width and clutch size of the wolf spider *Pardosa palustris* (Linnaeus 1758) in general, and specifically for any variations between sampling years and along the elevational gradient. Additionally, we investigated d) separate differences in egg volume, clutch size, and prosoma width between sampling years and in relation to the elevational gradient.

We expected that higher elevations and years with less favourable environmental conditions (e.g. lower temperatures) would lead *P. palustris* to produce larger eggs but smaller clutches.

Materials and methods

Study area

The study was conducted in central Norway (61°53'N, 9°15'E; Vågå, Oppland; Fig. 1a) in early July of 2006, 2010, and 2014 along an elevational transect. To cover most of the elevational range of the species at Blåhø, the elevational transect extended from 690 m above sea level (a.s.l.) to 1460 m a.s.l. and included nine sampling sites. These nine sites consisted of sub-alpine sites ($n=4$) below and alpine sites ($n=5$) above the treeline, the latter of which were divided into low-alpine ($n=3$) and middle-alpine ($n=2$) sites. According to an elevational decrease of approx. 0.6 °C for every 100 m of increase (Barry 2008), the overall decrease in temperature along our sampled elevational gradient corresponded to approximately 4.6 °C. Based on this elevation–temperature dependency, we used higher

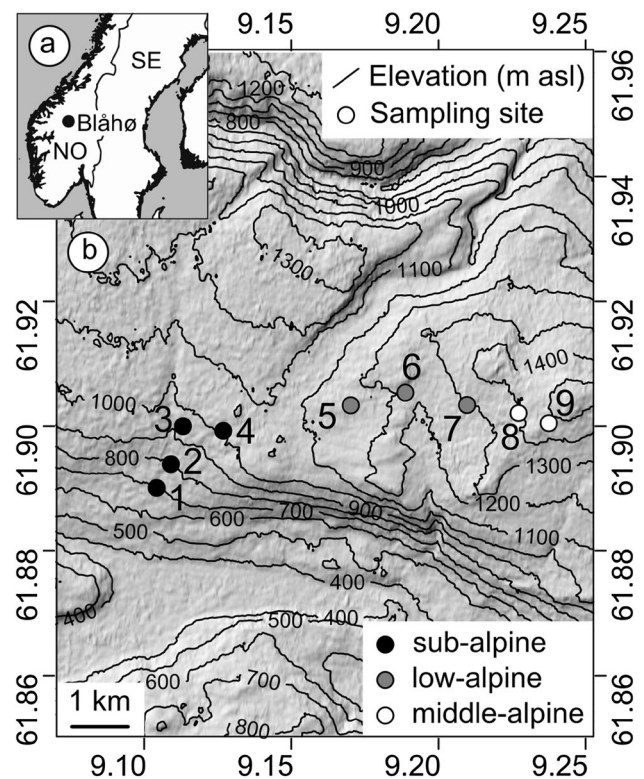


Fig. 1 a Location of the study site (Blåhø 1617 m a.s.l.) and b distribution of the nine sampling sites on the mountain slopes (WGS 84). Elevation data were extracted from ASTER GDEM. ASTER GDEM is a product of METI and NASA

elevations as a proxy for more extreme environmental conditions. The alpine environment starts above the treeline located at approximately 1030 m a.s.l., with a transition zone between the low-alpine and middle-alpine belts at approximately 1350 m a.s.l. Sampling sites were chosen for their elevational range and the typical aspects of lycosid-preferred habitats.

Pardosa palustris is found in high abundance in open and sunny habitats; consequently, all of the sampling sites were open, south-facing slopes (e.g. Hein et al. 2015). Shrub and heather communities dominate the vegetation at the low-alpine sampling sites, while graminoid species dominate the vegetation at the middle-alpine sampling sites (Fig. 1b).

The study area is located in the most continental part of Norway and has a very low annual precipitation of approximately 300–400 mm in the valleys (~350 m a.s.l.) and of 500–600 mm at the higher elevated sites (~1100 m a.s.l.). According to Moen (1998), the study area is a part of the “weak continental section” in Norway. During summer, the low-alpine belt is characterized by an average of 16 (min = 13, max = 19.3) snow-free weeks compared to only 11 (min = 7, max = 14.6) snow-free weeks in the middle-alpine belt. These values are based on weather station data from 2010–2017, and the average, minimum, and maximum values, including the following four different locations, were calculated: A = ridge, B = depression, C = south-facing slope, and D = north-facing slope in the low-alpine belt at approximately 1100 m and the middle-alpine belt at approximately 1400 m. The study area has an average of 150–170 days with temperatures ≥ 5 °C, and the annual average temperature is approximately 6 °C (Moen 1998).

Spider data

The lycosid wolf spider *P. palustris* has a holarctic distribution (World Spider Catalog 2016) and is one of the most common lycosid species in the study area (Hein et al. 2014b). It is present in a large variety of open habitats from coastal regions to high mountain areas (Hänggi et al. 1995). *Pardosa palustris* has a biennial life cycle in the lowlands and central Europe (Steigen 1975; Almquist 2005). However, Steigen (1975) concludes this species would overwinter three times as juveniles at the higher elevations of Hardangervidda in southern Norway. This is probably the result of a prolonged life cycle at higher elevations because of their slower growth in cold environments (Atkinson 1994; Danks 2004). After copulation, *P. palustris* females commonly produce two egg sacs (and sometimes three; see Bayram 2000), but the second and third egg sacs have much smaller clutch sizes and high mortality rates; they are therefore assumed to not contribute to the population (e.g. Kessler 1973; Steigen 1975). In our study area, we observed that second egg sacs

are not produced before the beginning of August, which is in agreement with Steigen’s (1975) observations.

In early July, shortly after females with their first egg sacs were spotted, they were hand sampled along the elevational transect. One person sampled each of the nine sampling sites for a maximum of 1 h per day for a maximum of three consecutive days. This enabled the comparison of the production of first egg sacs only during the study years and reduced possible biases by varying sampling dates. Because of time-dependent sampling, there are uneven sample sizes for each sampled site and year (Online Resource 1).

Each female and its egg sac were stored separately in 70% ethanol. We used prosoma width as a proxy for female body size because it is a powerful trait when dealing with developmental stage and overall spider size (Hagstrum 1971; Jakob et al. 1996; Moya-Laraño et al. 2008). The number of eggs in each sac was counted to determine individual specific clutch sizes. Egg sacs containing post-embryos (e.g. Breene 2005) were excluded (2006, $n = 21$; 2010, $n = 8$; 2014, $n = 5$). To determine the prosoma width and egg size, each female and ten randomly chosen eggs (e.g. Hendrickx et al. 2003; Pétilion et al. 2009) from the individual’s egg sac were digitally photographed with a Sony Cybershot camera using a binocular lens with 100 \times magnification. Images were used to measure the female prosoma width, egg length, and egg width with an accuracy of 0.01 mm. The egg size (volume mm^3) was then calculated as described by Hendrickx et al. (2003), using the egg length and width measurements.

Temperature data

We used the temperature data from a local weather station situated at 1100 m a.s.l. to investigate whether the observed variations between the three reproductive periods may be related to, or may be influenced by, annual temperature differences. The temperature data were obtained from a weather station established in the study area in 1994 that is situated at a ridge site in the low-alpine belt. The weather station is part of the Long-Term Alpine Ecological Research (LTAER) project [see Löffler (2002) for further details]. The calculated temperature sums, which are the cumulative hours with a mean 2-m air temperature > 0 °C ($\#h_{>0}$), and degree days were used as a proxy for the local climate for the three focal reproductive periods. The degree days were calculated following the basic equation using McMaster and Wilhelm’s (1997) 2nd method.

To account for the unclear timing of adulthood and thus the ability to reproduce, we calculated the $\#h_{>0}$ and number of growing degree days (GDD; $T_{base} = 0$) separately for the following three different periods:

- (1) From 1 January until the first day of sampling in the trap year $\#h_{>0}$ (temp^0) and GDD ($T_{base} = 0^0$);

- (2) From 1 January of the previous year until the first day of sampling $\#h_{>0}$ (temp^{-1}) and GDD ($T_{\text{base}} = 0^{-1}$); and
- (3) From 1 January of the two years previous until the first day of sampling $\#h_{>0}$ (temp^{-2}) and GDD ($T_{\text{base}} = 0^{-2}$).

The calculated and plotted data for $\#h_{>0}$ and GDD for the three respective periods are provided in Online Resource 2.

Analysis

An analysis of covariance was performed on linear mixed-effects models (mixed-effects ANCOVA) to investigate objectives a–c, as outlined in the Introduction. Additionally, we tested for d) significant differences in mean values (\pm standard error of the mean) of egg volume, clutch size, and prosoma width between sampling years and elevation zones using Tukey's honest significant difference test (Tukey's HSD test, $p < 0.05$) performed on separate models.

To explore possible synergistic effects with elevation on a trade-off between clutch size and egg volume, a relationship between body size (prosoma width) and egg volume, and a relationship between body size and clutch size, we assigned sampling sites within 690–1010 m a.s.l. to the sub-alpine zone, sites within 1170–1290 m a.s.l. to the low-alpine zone, and sites within 1390–1460 m a.s.l. to the mid-alpine zone (each sampling site represents the core area of each elevation zone). As a result of uneven sampling along the elevational gradient (Fig. 1b), we explicitly opted for these three different elevation zones because of prominent habitat changes in the transition from the treeline to the low-alpine zone (at approx. 1030 m a.s.l.) and from the low-alpine to the mid-alpine zone (at approx. 1350 m a.s.l.), which resulted in nonlinear variation in reproductive traits as shown by Hein et al. (2015). Treating elevation as a categorical variable is advantageous because we are able to specify, based on slope estimates, if and how a general effect of clutch size and prosoma width on the response parameter becomes weaker or stronger by moving from the sub- to the mid-alpine zone.

The models tested for a trade-off between clutch size and egg volume included clutch size, sampling year, and elevation zone as fixed effects and the specific sampling sites as a random effect. The latter is crucial to generate more robust results by accounting for trait similarities of female spiders sampled at a specific elevation zone. In addition to these single explanatory variables, separate interactions of clutch size with sampling year and elevation zone, respectively, were added as fixed effects. Both sampling year (2006, 2010, and 2014) and elevation zone (sub-alpine, low-alpine, and mid-alpine) were entered as categorical variables with three levels each. The final model was identified using significance levels revealed by

stepwise backward selection (ANOVA-based) in conjunction with the Akaike information criterion (AIC). Fixed effects were kept that were significant ($p < 0.05$), justifying an increase in model complexity by increasing explanatory power.

The mixed-effects ANCOVA for a relationship between body size (prosoma width) and egg volume and a relationship between prosoma width and clutch size followed the same structure and included prosoma width, sampling year, elevation zone, and their interactions with prosoma width as fixed effects, whereas sample sites served as a random effect. Models were also simplified by the procedure of a stepwise backward selection. In addition to the significance levels of the explanatory variables for each of the final (simplified) models (a–c), the marginal R-squared (explained variance of fixed effects only) is provided as a measure for the overall explanatory power.

The interactions of sampling year and/or elevation zone with clutch size and prosoma width are graphically displayed by separate model predictions for each elevation zone in each sampling year. The strength in interactions is supported by estimates on slopes of the final models, which are listed together with the model structure. Herein, the mean rates of change in response variables caused by sampling year as a single predictor were referenced to the baseline year 2006 and those of elevation zone to the mid-alpine zone, potentially representing the harshest environmental conditions among the sampling sites. The slope estimates on interactions provide the opportunity to specifically quantify if and how strongly the general effect of a certain explanatory variable (clutch size or prosoma width) varies between sampling years and elevation zones (by calculating the sum between the slope estimate of the single explanatory variable and those of its interaction with sampling year or elevation zone, respectively).

In order to further investigate variations in an egg size versus number trade-off, we tested for significant differences in egg volume, clutch size, and prosoma width between sampling years and elevation zones. The models to address this objective included sampling year or elevation zone as categorical variable (fixed effect) and sample sites as a random effect. If the explanatory variable was significant ($p < 0.05$, tested by ANOVA), Tukey's HSD test was subsequently applied, comparing the three different sampling years and elevation zones with each other. This procedure was repeated for the response variables, i.e. egg volume, clutch size, and prosoma width, separately.

The assumptions of normally distributed residuals and homogeneity of variance were consistently met for each of the models (a–d) and all data analyses were conducted using the R environment for statistical computing (R Core Team 2017).

Results

A total of 241 *P. palustris* females with egg sacs containing eggs were sampled (2006, $n = 66$; 2010, $n = 101$; 2014, $n = 74$) along the elevational transect (Online Resource 1). The sampled *P. palustris* egg sacs showed no signs of parasitism.

Mixed-effects ANCOVA revealed a significant interaction with sampling year for the trade-off between clutch size and egg volume (Table 1). This trade-off was strongest in 2014 (Fig. 2a), where the generally negative effect of clutch size changed from 0.0005 to 0.0022 mm³ decrease in mean egg volume per increase in clutch size of 1 (sum between the slope estimate of clutch size as a single explanatory variable and the slope estimate of clutch size

in interaction with sampling year 2014; Table 2). Compared to 2014, the trade-off in 2010 is more than two times lower, with a decrease of only 0.0009 mm³ in mean egg volume per increase in clutch size of 1 (Table 2). Overall, the fixed effects in the model on the trade-off between clutch size and egg volume account for an explained variance of 53% (marginal $R^2 = 0.53$; Table 1). As indicated by the significant variation in egg volume between sampling years (Table 3), the trade-off increase arises from the significantly higher egg volume in the year 2014 compared to the other sampling years (Tukey's HSD test with $p < 0.05$; Fig. 2d).

The relationship between prosoma width and clutch size was found to interact significantly with elevation zone (Table 1). In particular, this relationship appeared to be more pronounced in the sub-alpine zone with a stronger

Table 1 Mixed-effects ANCOVA on (a) the trade-off between egg volume and clutch size, and the relationships between (b) egg volume and prosoma width and c) clutch size and prosoma width in interaction (x) with sampling year and elevation zone

	Degrees of freedom	Sum of squares	Mean square	F-value	<i>p</i> -value
<u>Response variable: Egg volume</u>					
<i>Model a)</i>					
<u>Fixed effects ($R^2_m = 0.53$)</u>					
Clutch size	1	0.017	0.017	8.521	0.004 **
Sampling year	2	0.083	0.042	20.782	< 0.001 ***
Elevation zone	2	0.030	0.015	7.608	0.025 *
Clutch size × Sampling year	2	0.020	0.010	4.900	0.008 **
Residuals	231	0.459	0.002		

<i>Model b)</i>					
<u>Fixed effects ($R^2_m = 0.51$)</u>					
Prosoma width	1	0.021	0.021	10.430	0.001 **
Sampling year	2	0.353	0.177	88.922	< 0.001 ***
Elevation zone	2	0.027	0.014	6.882	0.030 *
Residuals	233	0.458	0.002		
<u>Response variable: Clutch size</u>					
<i>Model c)</i>					
<u>Fixed effects ($R^2_m = 0.56$)</u>					
Prosoma width	1	6945.40	6945.40	133.247	< 0.001 ***
Sampling year	2	618.30	309.20	5.931	0.003 **
Elevation zone	2	217.40	108.70	2.086	0.127
Prosoma width × Elevation zone	2	400.40	200.20	3.841	0.023 *
Residuals	231	11931.40	49.51		

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

Different models on the same response variable are separated by a dashed line, models on different response variables by a solid line. Marginal R-squared (R^2_m) is given as the explained variance of fixed effects only.

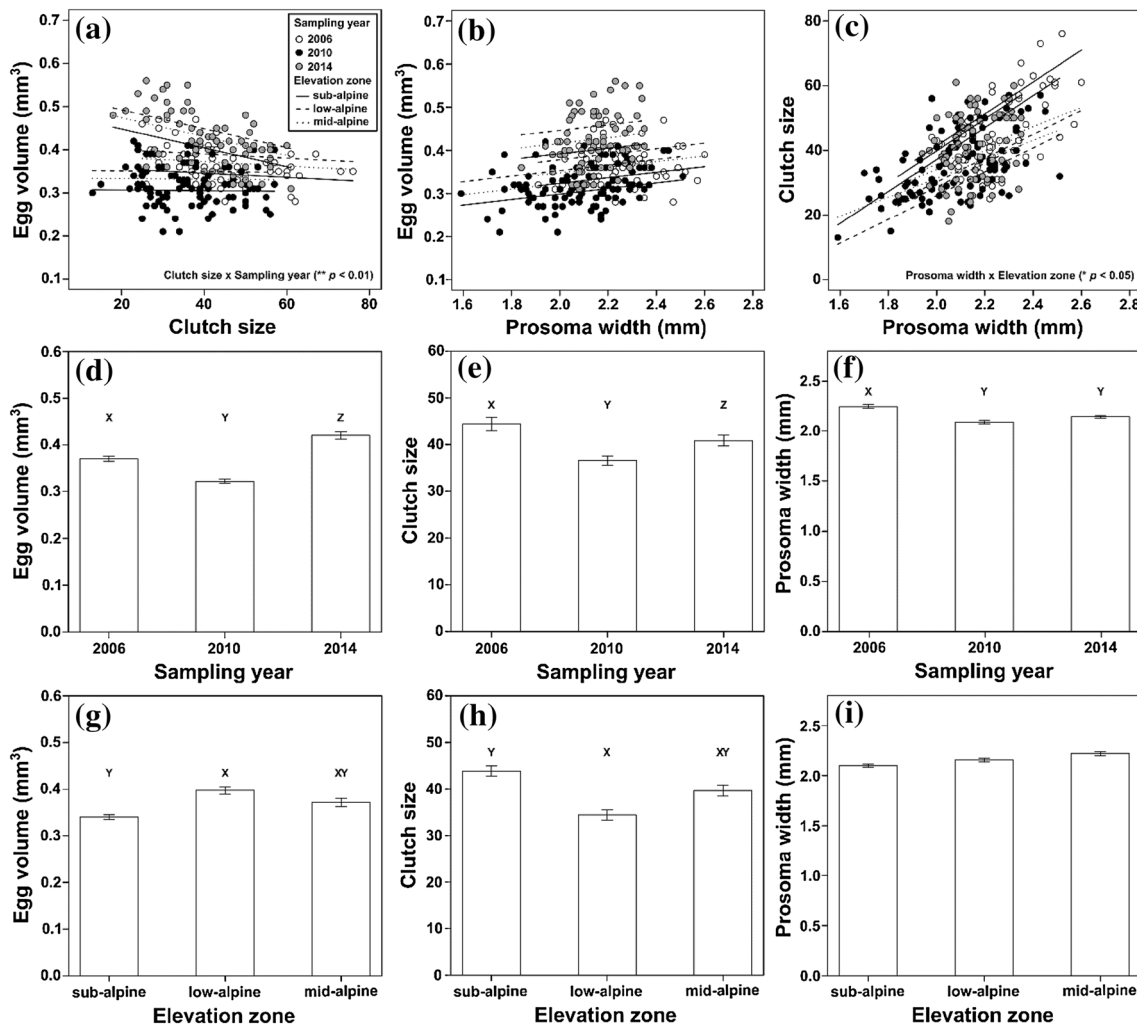


Fig. 2 Scatterplots on **a** the trade-off between clutch size and egg volume, **b** the relationship between prosoma width and egg volume, and **c** the relationship between prosoma width and clutch size. Prediction lines are based on final models (see Table 1) and given for each elevation zone (sub-alpine: sites within 690–1010 m a.s.l.; low-alpine: sites within 1170–1290 m a.s.l.; mid-alpine: sites within 1390–1460 m a.s.l) in each sampling year (2006, 2010, and 2014) to display significant interactions (x) identified by the mixed-effects ANCOVA. The trade-off between clutch size and egg volume is strongest in

2014, whereas the positive relationship between prosoma width and clutch size is more pronounced in the sub-alpine zone and weakens with elevation (as indicated by decreasing slope steepness). For the relationship between prosoma width and egg volume, no interaction was found with the sampling year or with the elevation zone (as indicated by parallel slopes). Significant contrasts in the reproduction traits (mean \pm standard error of the mean) between (**d–f**) sampling years and (**g–i**) elevation zones are indicated by different letters (X, Y, Z; based on Tukey's HSD test with $*p < 0.05$)

increase of the generally positive effect of prosoma width on clutch size from 29.38 to 49.35 (increase in mean clutch size per increase in prosoma width of 1 mm; Table 2) compared to the low-alpine zone where it increased to 36.82 (Table 2). Thus, the strength of the relationship between the prosoma width and clutch size seems to weaken with elevation, which is indicated by the decrease in slope steepness from the sub- to the mid-alpine zone (Fig. 2c). The total explained variance of the fixed effects amounts to 56% for this model (marginal $R^2 = 0.56$; Table 1). The significant variation in clutch size between elevation zones (Table 3) revealed that clutch size was increased in the

sub-alpine zone (Tukey's HSD test with $p < 0.05$; Fig. 2h). However, prosoma width remained constant across all elevation zones (Table 3; Fig. 2i). The combination of both the increased clutch size in the sub-alpine zone and constant prosoma width possibly led to the more pronounced relationship as indicated by Fig. 2c.

The relationship between prosoma width and egg volume is independent of sampling year and elevation zone as indicated by the parallel slopes of the model (Fig. 2b). However, single predictor variables were significant and explained 51% of the variance (marginal $R^2 = 0.51$; Table 1).

Table 2 Intercept and slope estimates (plus standard errors) of fixed effects and the structure of final models (including the random effect of sample sites) for (a) the trade-off between egg volume and clutch size, (b) the relationship between egg volume and prosoma width, and (c) the relationship between clutch size and prosoma width in interaction (x) with sampling year and elevation zone

<i>Model a):</i> Egg volume ~ Clutch size + Sampling year + Elevation zone + Clutch size x Sampling year + (1 Sample sites)		
	<u>Estimate</u>	<u>Standard error</u>
Intercept	0.3921	0.0252
<u>Fixed effects</u>		
Clutch size	-0.0005	0.0005
Sampling year 2010	-0.0574	0.0290
Sampling year 2014	0.1261	0.0308
Elevation zone (low-alpine)	0.0181	0.0130
Elevation zone (sub-alpine)	-0.0263	0.0122
Clutch size x Sampling year 2010	-0.0004	0.0007
Clutch size x Sampling year 2014	-0.0017	0.0007
<i>Model b):</i> Egg volume ~ Prosoma width + Sampling year + Elevation zone + (1 Sample sites)		
Intercept	0.2197	0.0481
<u>Fixed effects</u>		
Prosoma width	0.0643	0.0199
Sampling year 2010	-0.0250	0.0079
Sampling year 2014	0.0681	0.0081
Elevation zone (low-alpine)	0.0299	0.0174
Elevation zone (sub-alpine)	-0.0244	0.0165
<i>Model c):</i> Clutch size ~ Prosoma width + Sampling year + Elevation zone + Prosoma width x Elevation zone + (1 Sample sites)		
Intercept	-23.193	14.600
<u>Fixed effects</u>		
Prosoma width	29.384	6.414
Sampling year 2010	-4.215	1.278
Sampling year 2014	-1.535	1.301
Elevation zone (low-alpine)	-20.230	18.503
Elevation zone (sub-alpine)	-34.132	16.848
Prosoma width x Elevation zone (low-alpine)	7.443	8.328
Prosoma width x Elevation zone (sub-alpine)	19.965	7.632

Discussion

Our results suggest that egg volume is temporally and spatially more variable than expected. The expected trade-off between clutch size and egg volume in the three reproductive periods was observed, meaning that larger eggs

accompanied smaller clutch sizes and vice versa. This trade-off has been widely argued to be a consequence of limited resource availability (Smith and Fretwell 1974). However, our study during these three reproductive periods revealed that under certain environmental conditions, bigger eggs could be produced almost independent of the mother’s size.

Table 3 ANOVA for models on (d) the contrast of egg volume, clutch size, and prosoma width between sampling years and elevation zones

	Degrees of freedom	Sum of squares	Mean square	F-value	<i>p</i> -value
<u>Response variable: <i>Egg volume</i></u>					
<i>Models d</i>					
Sampling year	2	0.369	0.185	88.951	< 0.001 ***
Residuals	236	0.479	0.002		
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Elevation zone	2	0.045	0.022	6.173	0.036 *
Residuals	236	0.848	0.004		
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<u>Response variable: <i>Clutch size</i></u>					
Sampling year	2	3743.00	1871.50	20.970	< 0.001 ***
Residuals	236	20607.77	85.51		
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Elevation zone	2	1841.20	920.62	8.728	0.023 *
Residuals	236	11931.43	49.51		
<hr/>					
<u>Response variable: <i>Prosoma width</i></u>					
Sampling year	2	0.800	0.400	18.672	< 0.001 ***
Residuals	236	4.960	0.021		
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Elevation zone	2	0.201	0.105	4.284	0.074
Residuals	236	5.720	0.024		

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

Different models on the same response variable are separated by a dashed line, and models on different response variables by a solid line. Only significant models (of at least * $p < 0.05$) were used to perform Tukey's HSD test.

Thus, the largest egg volumes (2014) are not accompanied with the largest females, while clutch size is always dependent on the mother's size. Previous studies have shown that variations in body size of lycosid spiders are related to the timing of snowmelt and environmental gradients of resource availability (Høye et al. 2009; Bowden et al. 2013). Consequently, these changes in body size will lead to alterations in reproductive output.

A linear relationship between increasing elevation and more extreme environmental conditions was not found in our study because body size and reproductive rate in *P. palustris* were not significantly affected at higher elevations. This supports previous findings where spatial patterns of reproductive traits along an elevational gradient could not be generalized, because elevation-related effects are overlain by fine-scale site conditions (Bowden et al. 2013; Hein et al. 2015). In our data, changes in the habitat type from sub-alpine to low-alpine and from low-alpine to middle-alpine seem to be responsible for variations in the reproductive traits of *P. palustris*. Franz (1979) stated that there can be no bigger contrast than the transition from sub-alpine to alpine conditions. Accordingly, several studies

showed the importance of the treeline and the concomitant changes in the environmental conditions for spider distribution, diversity, and competition within the respective habitat types (Hauge and Refseth 1979; Frick et al. 2007; Muff et al. 2009). Additionally, the transition from the low-alpine zone to the middle-alpine zone is characterized by a rather abrupt change from shrub-dominated to more open and graminoid-dominated vegetation. Daily maximum soil temperatures in the middle-alpine zone regularly exceed temperatures in the low-alpine zone during summer, because there is less vegetation coverage and more open ground (Löffler et al. 2008; Wundram et al. 2010). Consequently, the environmental conditions for *P. palustris* might be more favourable at higher elevations than at lower elevations.

When comparing the three different reproductive periods studied, climatic variations in the number of GDDs and the $\#h_{>0}$ were observed. It is widely acknowledged that an increased number of degree days has a strong impact on the development of ectotherms (Blanckenhorn 1997; Dixon et al. 2009; Chezik et al. 2013), but because of the small sample size, the quantification of temperature-dependent effects on the reproductive traits in *P. palustris* was not

possible. However, the specific environmental conditions in the respective reproductive periods had a more direct than indirect effect on egg size as a result of the mother's size. Additionally, the egg sizes in 2010 were significantly smaller than those in the other 2 years and were accompanied by the lowest GDD and $\#h_{>0}$ [except $\#h_{>0}$ (Temp^0)] values during the reproductive periods. This contradicts our original expectation that egg volume would decrease and clutch size increase in response to higher temperatures at lower elevations. We expected a Bergmann's cline in sensu lato in the egg size of *P. palustris* (Blackburn et al. 1999; Chown and Gaston 2010; Shelomi 2012), but instead the results showed an increase in egg volume in the respective reproductive periods. This is opposite of Bergmann's cline (e.g. Mousseau 1997; Blanckenhorn and Demont 2004). However, interpretation of the results might be affected by spatial pseudo-replication (e.g. Oksanen 2001), because our sampling is nested along the elevational gradient and measured repeatedly instead of effectively replicated.

Spider starvation is a commonly observed phenomenon in the field (Wise 1993; Brown et al. 2003). Generally, higher temperatures and prolonged summer seasons allow for higher activity levels (Høye and Forchhammer 2008; Hein et al. 2014a) and foraging rates in ectothermic species (Willmer et al. 2005; Høye et al. 2009). Ford (1978) also reported increased activity in the lycosid spider *Pardosa amentata* (Clerck 1757) in response to higher temperatures. Because of higher overall temperature sums and prolonged summer seasons, the spiders would have access to more resources earlier in the year, which enables them to accumulate more reserves for egg production (Vollrath 1987). This is in concordance with Riechert and Tracy (1975), who reported an increase in egg size in response to higher prey availability. Accordingly, Samu and Biro (1993) showed that wolf spiders could modify their feeding behaviour with multiple killings and increased feeding when higher prey densities were present. A similar change of food web-related interactions between the spiders and their prey may have occurred at our site when the overall temperature sums and GDDs increased, resulting in *P. palustris* investing in larger eggs, with no decrease in clutch size. However, an increase in egg volume is limited because there has to be a threshold at which female spiders no longer invest in larger egg volumes. This threshold could be related to the prey abundance rate at which multiple killings become no longer worth the additional energetic effort, because the likelihood of food limitations on the offspring after dismounting is reduced, or it could be related to egg storage capacity that is limited by the mother's size.

Generally, larger females should have a higher potential fecundity than smaller females (e.g. Stearns 1992; Roff 2002; Steiger 2013). We found this relationship to be highly significant in our study. Consequently, lycosid

spiders that grow larger in response to prolonged summer seasons should have higher reproductive rates (Vertainen et al. 2000; Høye et al. 2009). Clutch size varied consistently with prosoma width, but we found no such interdependence between egg volume and female body size in our study. This agrees with some of Kessler's (1971) observations, who found no change in the number of eggs produced by *P. palustris*, but did find a tendency to produce lighter eggs during food shortages. This effect also might have been the reason for smaller egg sizes in response to the environmental conditions in our study.

A recent study by Verdeny-Vilalta et al. (2015) showed that actively foraging spider species have increased egg volumes compared with "sit and wait" foragers. This suggests that higher reproductive rates may be linked to higher activity in response to higher temperatures, along with the resulting higher foraging rates. Accordingly, more resources lead to larger eggs without the influence by the mother's size in *P. palustris*. Larger eggs commonly result in larger, healthier offspring that have a higher starvation resistance (Simpson 1995; Fox and Czesak 2000; Grinsted et al. 2014) and more resistance to desiccation (Fischer et al. 2006). Larger offspring are also highly advantageous in terms of intraguild predation, because they are less vulnerable as prey and probably more successful as predators (Rickers and Scheu 2005; Segers and Taborsky 2011; Verdeny-Vilalta et al. 2015).

We assume the rapid adjustment of egg size to inter-annual differences in environmental conditions by this generalist species supports the findings of extensive phenotypic plasticity in *P. palustris*'s reproductive traits (Kessler 1971; Hein et al. 2015). For example, when Ameline et al. (2017) compared the reproductive traits of generalist and specialist lycosid species in Arctic and temperate habitats, they found that specialist species in Arctic habitats invested more into the clutch size than did generalist species.

Species with high phenotypic plasticity will be more likely to persist in response to climate change (Scharf et al. 2010; Gardner et al. 2011). Our results illustrate that a generalist predator species such as *P. palustris* could also persist, and to some extent, benefit from rising temperatures by achieving increased reproductive success. Further research is needed to confirm whether the observed variations in the trade-off between egg number and egg size in our study can be applied to other generalist species, and how specialist species in cold environments react to changes in abiotic conditions such as higher temperatures and changes in snow-cover duration.

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