

## Comparison of reproductive traits between two salt-marsh wolf spiders (Araneae, Lycosidae) under different habitat suitability conditions

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### Abstract

Salt-marsh invasions by the grass *Elymus athericus* (Poaceae) recently transformed usual areas dominated by *Atriplex portulacoides* (Chenopodiaceae) into homogeneous meadows. Two wolf spider species, *Pardosa purbeckensis* and *Arctosa fulvolineata*, show contrasting densities and habitat preferences in salt marshes (respectively dominant and co-dominant ground-living spiders) and oppositely respond to the grass invasion. This allowed us to test whether invasive species that alter habitat structure affect reproduction in addition to previously recorded changes in density. Reproductive traits (female mass, cocoon mass, number and volume of eggs, hatched cocoon as a proxy of reproduction date) were studied in both invaded and natural salt marshes during 2007 and 2008 in the Mont St-Michel Bay (France). In both species, reproductive outputs (cocoon mass) were higher in optimal habitats and volume of eggs was found to be independent from female mass, whereas the latter significantly influenced the number of eggs. In *A. fulvolineata*, lower reproductive outputs due to less numerous although larger eggs were found in suboptimal habitats whereas the opposite pattern was found in optimal habitats, showing the existence of plastic phenotypic trade-offs in habitats of different qualities. In *P. purbeckensis*, despite differences in population size among habitats, no reproductive trade-off was found. This study thus shows that two sympatric species belonging to the same family can differ in reproductive strategies and phenotypic plasticity under changes in habitat suitability.

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**Keywords**

Inter-specific comparison; lycosid; halophilic species; fitness; plant invasion

**Introduction**

Intertidal salt marshes, habitats submitted to periodical flooding during tides, are among the rarest ecosystems in the world, covering less than 0.01% of Earth (De-sender and Maelfait, 1999; Lefeuvre et al., 2003). In Europe, their surface strongly declined during the last decades, reinforcing the conservation interest due to their original flora and fauna (Bakker et al., 2002). Since twenty years, salt marshes have been invaded by the nitrophilous grass *Elymus athericus* (Poaceae, Valéry et al., 2004), probably due to increases in soil nitrogen (via the accumulation of nitrogenous compounds in the plant: Leport et al., 2006) and/or to the abandonment of cultural practises (e.g. Esselink et al., 2000). Although *Elymus athericus* is a native species, usually growing in the upper parts of salt marshes, we hereby use the adjective native invasive, as the strong dominance of a single species can be assimilated to an invasion in this case (Valéry et al., 2009a). In the Mont Saint-Michel bay, this plant covers now 35% of the whole marsh (to be compared with 3% in 1984) with a current progression of 105 ha/year (A. Radureau and L. Valéry, unpublished data, 2007). Invaded areas mainly differ from natural habitats (usually dominated by *Atriplex portulacoides*, Chenopodiaceae, in ungrazed middle marshes) by their deeper litter and by their taller plant cover. Thus, this invasion has completely changed the structure of the environment and creates a unique experimental design where two contrasted habitats coexist at a small scale. Such invasions, occurring in many West-European sites (Bockelmann and Neuhaus, 1999), modify biodiversity as well as ecosystem functioning and can thus be used as model systems for studying general ecological and evolutionary processes (Valéry et al., 2009b).

Among salt-marsh terrestrial arthropods, spiders constitute a major group in terms of abundance and diversity (Baert and Maelfait, 1999; Finch et al., 2007; Pétilion et al., 2008), with well known bio-indicative qualities (Marc et al., 1999). Some stenotopic species are also known to withstand flooding and salinity, by means of physiological, behavioural or morphological adaptations (e.g. Foster and Treherne, 1976; Irmiler et al., 2002; Pétilion et al. 2009a). Spiders have been shown to strongly react to invasions by *Elymus*, notably exhibiting changes in species richness (Pétilion et al., 2005a) and trophic guilds (Pétilion et al., 2006) within invaded habitats. At population level, *E. athericus* habitats are optimal for the lycosid species *A. fulvolineata*, that species exhibiting higher reproductive outputs, with smaller and more numerous eggs in invaded habitats (Pétilion et al., 2009b). These differences in reproductive outputs and life history strategies were assumed to be driven by phenotypic plasticity in female mass and resource allocations, respectively. Among spiders, the family of Lycosidae presents the advantage of including closely related species with similar foraging strategies and overlapping patterns of microhabitat use (DeVito et al., 2004).

In this study, we compared the reproductive traits (size of reproductive outputs as a proxy of reproductive fitness, number and size of eggs, percentage of cocoons with hatched eggs as a proxy of reproduction date) of *A. fulvolineata* with those of the other dominant lycosid *Pardosa purbeckensis* in both natural and invaded habitats. As both species belong to the same family and as they are sympatric, occurring in salt-marsh habitats in high numbers (co-dominant species of the ground-living spider assemblages of the Mont Saint-Michel bay: Pétilion et al., 2006), we hypothesize the existence of a plastic reproduction in *P. purbeckensis* as in *A. fulvolineata*. We thereby expect: (i) Higher reproductive outputs in optimal habitats compared to sub-optimal habitats. According to the relation between population size and habitat suitability at low to moderate densities (e.g. Schilling, 2005), *A. portulacoides* habitat is expected to be optimal for *P. purbeckensis* (Pétilion et al., 2005b). Moreover (ii) related size-number of eggs trade-off (in lycosid species, see e.g. Brown et al., 2003; Walker et al., 2003) and (iii) earlier hatchings in habitats with bigger eggs due to a faster development (Fox and Czesack, 2000) are expected to occur.

## Materials and methods

### *Field and laboratory data collection*

Sampling took place within the Mont St-Michel Bay (NW France), at the Vivier-sur-Mer location (48°60'N, 1°78'W). Spiders were sampled in invaded (dominated by *E. athericus*) and natural (dominated by *A. portulacoides*) salt-marsh habitats, located at the same distance from the dike (350 m) due to the existence of a salinity gradient across the salt marsh, which strongly affects the distribution ranges and abundances of spider species (Pétilion et al., 2010).

The presence of cocoon was regularly checked and samplings took place two weeks after the first observations of cocoons for ensuring to sample only first eggs, although a second reproduction has not been observed for those species (one single peak of activity: e.g. Schaefer, 1972; Harvey et al., 2002). Spiders were first collected the 4<sup>th</sup>, May 2007 for measurements of female mass and size and number of eggs (during the peak of reproduction of the two species) and again the 30<sup>th</sup>, May 2008 to estimate the date of reproduction. 30 females of each species (*A. fulvolineata* (Lucas 1846) and *P. purbeckensis* (F.O.P.-Cambridge 1895)) were hand-collected with their egg-sac in both habitat types (as in Hendrickx et al., 2003a, b; Skow and Jakob, 2003; Pétilion et al., 2009b).

The percentage of cocoons with hatched eggs (detected by the presence of pulli within the cocoon) was determined for each species in both habitats and used as a proxy of the reproduction date.

All individuals were kept in ethanol 70° and their cocoons were put at 5°C to stop egg development until measurements. In laboratory, female body dry mass (generally used as an index of health condition for spiders: e.g. Jakob et al., 1996) and clutch mass were weighted to the nearest 0.1 mg. The number of eggs in each cocoon was counted and the length and width of ten eggs per cocoon were mea-

sured to the nearest 0.01 mm. Egg volume was calculated according to the formula: egg volume =  $\pi/6 * (\text{egg length}) * (\text{egg width})^2$  (Hendrickx and Maelfait, 2003).

### Data analysis

A regression analysis was conducted for testing the relationship between cocoon mass and female mass in both habitats. One-way ANOVA was used to determine if there was a significant difference in mean cocoon mass between habitats (natural vs. invaded as fixed factors). Cocoon mass data were  $\ln(x + 1)$  transformed to meet the assumptions of normality and homogeneity of variance. To assess differences in egg number and volume between habitats, ANCOVAs were realized using respectively number of eggs and egg volume as dependent variables, female mass as the covariate and habitat as the main factor. Homogeneity of the slopes of dependent-covariate relationships was tested with the ANCOVA design that analyzed the pooled covariate-by-factor interaction (García-Berthou, 2001). If the covariate-by-factor interaction was not significant (homogeneity of slopes in model 1), a standard ANCOVA (model 2) was used to test significant differences in dependent variables between habitats (i.e. differences in intercept by using the adjusted mean female body mass).

$\chi^2$  test was used to compare the percentage of hatched and non hatched eggs (i.e. presence of pulli within the cocoon) between suboptimal and optimal habitats for each species. For both analyses, the level of statistical significance used was  $P < 0.05$ . Results were expressed as means  $\pm$  S.E. Treatments were performed on R software (Ihaka and Gentleman, 1996, <http://www.r-project.org/>).

## Results

Independently from habitat type, cocoon mass was positively correlated to female mass for both *A. fulvolineata* and *P. purbeckensis* (Regression analysis, respectively: Cocoon mass =  $3.51 \times \text{Female mass} - 10.11$ ,  $R_{\text{adj.}}^2 = 0.78$ ,  $P < 0.001$ , 59 df and Cocoon mass =  $3.51 \times \text{Female mass} - 0.08$ ,  $R_{\text{adj.}}^2 = 0.60$ ,  $P < 0.001$ , 42 df). Cocoon mass were significantly higher in optimal habitats (table 1), for both *A. fulvolineata* (One-way ANOVA,  $F_{1,58} = 24.09$ ,  $p < 0.001$ ) and *P. purbeckensis* (One-way ANOVA,  $F_{1,58} = 11.52$ ,  $p = 0.001$ ). Female mass had a significant positive effect on number of eggs, but had no effect on egg volume for both *A. fulvolineata* and *P. purbeckensis* (tables 2 and 3). Habitat suitability had a significant effect on reproductive traits of *A. fulvolineata*, eggs being smaller and more numerous in optimal habitats (table 2, fig. 1). No significant effect of habitat suitability was found on the reproductive traits of *P. purbeckensis* (table 3, fig. 2), the volume and number of eggs being not statistically different between habitats. The percentage of hatched eggs was significantly higher in suboptimal habitat than in optimal one for *A. fulvolineata* (respectively 37.50% vs. 0%,  $\chi^2$  test,  $\chi^2 = 11.48$ ,  $p < 0.001$ , 1 df). No difference was found between the two habitat types for *P. purbeckensis* (60.71% vs. 66.67%,  $\chi^2$  test,  $\chi^2 = 0.21$ ,  $p = 0.646$ , 1 df) (fig. 3).

**Table 1.**

Reproductive traits of *Arctosa fulvolineata* and *Pardosa purbeckensis* in optimal and suboptimal habitats (mean  $\pm$  se, n = 30 per female and per habitat type).

	<i>Arctosa fulvolineata</i>		<i>Pardosa purbeckensis</i>	
	Optimal	Suboptimal	Optimal	Suboptimal
Mean female mass (mg)	33.5 $\pm$ 1.6	27.9 $\pm$ 0.9	7.1 $\pm$ 0.2	6.6 $\pm$ 0.2
Mean clutch mass (mg)	113.2 $\pm$ 5.1	82.0 $\pm$ 4.2	25.1 $\pm$ 0.7	21.4 $\pm$ 0.8
Mean number of eggs	147.7 $\pm$ 6.4	103.8 $\pm$ 5.7	56.9 $\pm$ 1.7	51.0 $\pm$ 2.2
Mean volume of eggs (mm <sup>3</sup> )	0.710 $\pm$ 0.004	0.744 $\pm$ 0.005	0.392 $\pm$ 0.008	0.381 $\pm$ 0.007

**Table 2.**

Relationships between the number and the volume of eggs and female mass in *Arctosa fulvolineata*.

Variable	Factor	F	df	P
Number of eggs	Model 1 (test for interaction)			
	Female mass	61.10	(1,56)	<0.001
	Habitat	4.73	(1,56)	0.033
	Female mass $\times$ Habitat	3.67	(1,56)	0.060
	Model 2 (no interaction)			
	Female mass	55.70	(1,57)	<0.001
	Habitat	17.12	(1,57)	<0.001
Volume of eggs	Model 1 (test for interaction)			
	Female mass	1.51	(1,55)	0.225
	Habitat	0.11	(1,55)	0.738
	Female mass $\times$ Habitat	0.25	(1,55)	0.616
	Model 2 (no interaction)			
	Female mass	1.27	(1,56)	0.264
	Habitat	7.38	(1,56)	<0.001

## Discussion

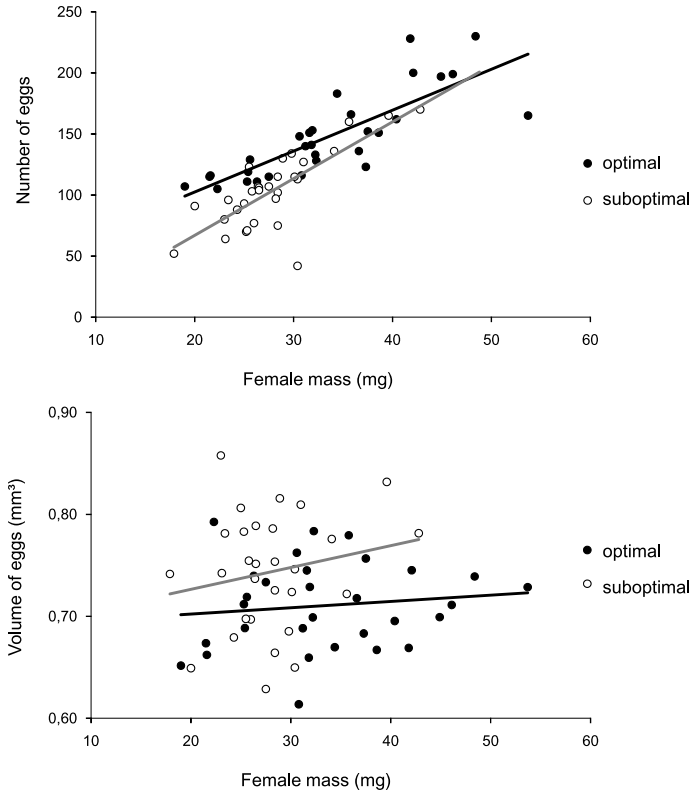
For both species, female mass were higher in optimal habitats, i.e. in *E. athericus* for *A. fulvolineata* and in *A. portulacoides* for *P. purbeckensis*. Cocoon mass was positively correlated to female mass and thus higher in optimal habitats, which confirms our assumption on patterns of habitat suitability. Brown et al. (2003) and Skow and Jakob (2003) also showed the same correlation between female and cocoon mass in the spiders *Pirata sedentarius* and *Holocnemus pluchei*, respectively. Previous studies carried out in the Mont St-Michel Bay salt-marshes showed that *P. purbeckensis* populations are very large in both habitat types, that species reaching some densities of 3.93 ind./m<sup>2</sup> in natural habitats and 1.37 ind./m<sup>2</sup> in invaded ones (Pétillon et al., 2005b). Differences in population sizes among habitat types can first be due to differences in food availability. Indeed, regarding potential prey, Acari and Amphipoda (*Orchestia gammarella* (Pallas, 1766)) densities were signif-

**Table 3.**Relationships between the number and the volume of eggs and female mass in *Pardosa purbeckensis*.

Variable	Factor	F	df	P
Number of eggs	Model 1 (test for interaction)			
	Female mass	49.72	(1,38)	<0.001
	Habitat	4.03	(1,38)	0.052
	Female mass × Habitat	3.71	(1,38)	0.062
	Model 2 (no interaction)			
	Female mass	55.20	(1,39)	<0.001
	Habitat	1.53	(1,39)	0.224
Volume of eggs	Model 1 (test for interaction)			
	Female mass	2.32	(1,51)	0.134
	Habitat	0.23	(1,51)	0.633
	Female mass × Habitat	0.26	(1,51)	0.613
	Model 2 (no interaction)			
	Female mass	2.10	(1,52)	0.153
	Habitat	0.22	(1,52)	0.643

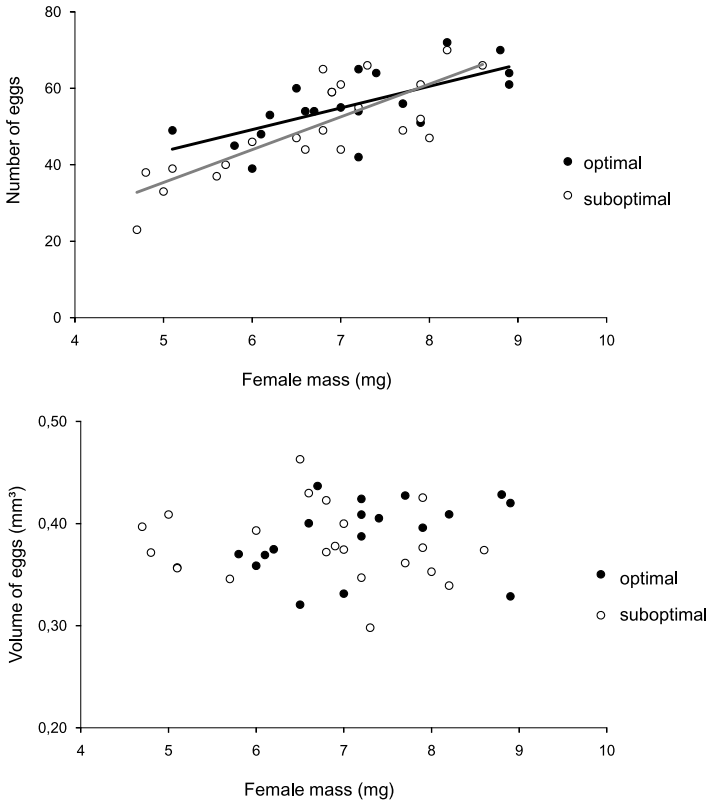
icantly lower in invaded areas, leading to a decrease in total pedofauna at these stations. Secondly, these differences can be linked to habitat structure, *P. purbeckensis* being a species reaching its highest densities in open habitats (young successional stages in salt marshes: Schaefer, 1974; Pétilion and Garbutt, 2008) which is the case of natural habitats in the Mont St-Michel Bay. *Pardosa purbeckensis* cannot yet be considered in a context of saturated populations, as reproductive fitness of that species positively co-varies with population density. When the carrying capacity is reached, habitat suitability is indeed predicted to decrease and fitness in two or more saturated patches of different qualities is equalized among all individuals (Fretwell and Lucas, 1970).

No size-number of eggs trade-off was found in *P. purbeckensis*. Habitat type affected neither the number and volume of eggs, nor the percentage of hatched cocoons. The absence of a size-number of eggs trade-off can be hidden by exchanges of individuals among habitats (high dispersal propensities of that species: Bonte et al., 2006). When spider relatives compete for the same resources, high dispersal rates are indeed favoured, leading to resource competition among non relatives (Bonte et al., 2007). This strategy takes part in spatial homogenization of fitness. Invaded and natural habitats are spatially close, which allows very mobile individuals, as in *P. purbeckensis*, to go from one habitat to the other. But in case of frequent exchanges of individuals by dispersal, equalization of female mass would be observed, which is not the case in our study. The absence of a size-number of eggs trade-off is likely to be due to a lack of reproductive plasticity, already reported in wolf spiders (Simpson, 1993) and in other arthropods (Fox and Czesack, 2000). Therefore, it can be concluded that the invasion of *E. athericus* has no influence on individual fitness of *P. purbeckensis*.

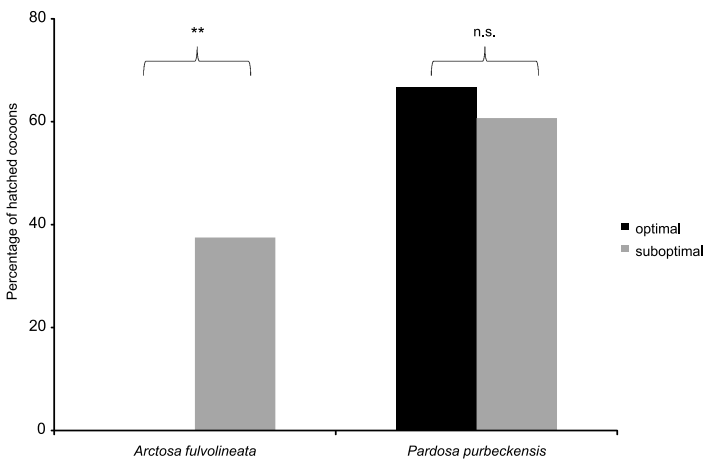


**Figure 1.** Number and volume of eggs vs. dry female mass in *Arctosa fulvolineata*. Black and grey lines: linear regressions in optimal and suboptimal habitats respectively.

On the contrary, *A. fulvolineata* has developed a size-number of eggs trade-off: eggs are smaller but more numerous in optimal habitats (*E. athericus*). The production of smaller but more numerous eggs actually results in a higher fecundity whereas bigger eggs will ensure a better survival for the offspring through predation and other pressures (Hendrickx et al., 2003b). *Arctosa fulvolineata* is a predator specialized upon Amphipods (Pétillon et al., 2009c), that can reach up to 300-800 individuals/m<sup>2</sup> in invaded and natural habitats (Laffaille et al., 2005). Comparing the densities of *A. fulvolineata* (i.e. 0.03 ind./m<sup>2</sup> in natural habitats and 0.43 ind./m<sup>2</sup> in invaded ones: Pétillon et al., 2005b) with those of its favourite prey suggests that intra-specific competition is low in both habitat types. Contrary to saturated conditions, animals inhabiting habitat with low densities are submitted to other fitness distributions (Greene and Stamps, 2001). Allee effects indeed occur when fitness increases as a function of density at low to moderate densities, and then declines at moderate to high densities. In heterogeneous environments, individuals can disperse among patches to find the most suitable one and then maximize their fitness (Poethke and Hovestadt, 2002) which can explain habitat selection by mobile foragers (e.g. Sutherland, 1983; Morris, 2003).



**Figure 2.** Number and volume of eggs vs. dry female mass in *Pardosa purbeckensis*. Black and grey lines: linear regressions in optimal and suboptimal habitats respectively.



**Figure 3.** Percentage of cocoons with pulli (hatched eggs) in optimal and suboptimal habitats for both lycosid species (n = 30 per female and per habitat type).

The trade-off observed for females of *A. fulvolineata* suggest that they are able to adjust their reproductive strategy according to habitat suitability in order to optimize their fitness in each habitat. Furthermore, we found a difference of hatching time (estimated by the percentage of hatched cocoons) between the two habitats only for this species. Females of *A. fulvolineata* thus reproduced earlier in the sub-optimal habitat, leading to a higher percentage of hatched eggs (and thus of pulli) in cocoon, probably to enhance offspring survival (Fox and Czesack, 2000, in lycosids: Reed and Nicholas, 2008). This early hatching can be attributed to a faster development because eggs were larger in natural (sub-optimal habitats). Difference in micro-climatic conditions between habitat types can also contribute to explain such pattern, suboptimal habitats being characterized by mean soil temperatures warmer than those in optimal habitats (J. Pétilion et al., unpublished data). The spitting spider *Scytodes pallida* hatches earlier in presence of the jumping spider *Portia labiata* because the risk of predation on egg-carrying females is more important than on eggless females (Daiqin, 2002). Hatching time can also be considered a plastic phenotypic trait that can be adjusted in response to predation or inter-competition risks.

Should *E. athericus* completely cover the Mont St-Michel bay salt-marshes in the coming years, at least in ungrazed areas, the question of organism and gene fluxes between natural and invaded habitats would become crucial. Further studies should investigate if differences in reproductive traits are only due to phenotypic plasticity or to, recent, genetic adaptations. Although this study is restricted in time (one season) and space (two populations), it shows inter-specific variations in reproductive strategies among two sympatric species.

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