Naturwissenschaften (2009) 96:1241–1246
DOI 10.1007/s00114-009-0589-7

SHORT COMMUNICATION

Plant invasion phenomenon enhances reproduction performance in an endangered spider

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Received: 11 December 2008 / Revised: 12 June 2009 / Accepted: 2 July 2009 / Published online: 21 July 2009

Abstract Current models in evolutionary ecology predict life history alterations in response to habitat suitability to optimize fitness. Only few empirical studies have demonstrated how life history traits that are expected to trade off against each other differ among environments. In Europe, many salt marshes have been recently invaded by the grass *Elymus athericus*. Previous studies however showed higher densities of the endangered spider *Arctosa fulvolineata* (Araneae: Lycosidae) in invaded salt marshes compared to natural habitats, which suggests a lower habitat suitability in the latter. The aim of this study was to determine if this emerging habitat (1) affects the amount of resource acquisition and (2) alters the balance between life history traits that are expected to trade off against each other in this stenotopic salt marsh species. As suggested by theoretical studies, an optimization of fitness by increasing egg size at the cost of decreasing fecundity in unsuitable (i.e., natural) habitats was expected. Females presenting cocoon were then collected in close invaded and natural salt marsh areas within the Mont Saint-Michel Bay (France). By considering female mass as covariate, cocoon mass, number of eggs, and egg volume were compared between both habitats. Clutch mass was strongly determined by female mass in both habitats. Clutch mass was however significantly smaller in the natural habitat compared to the invaded habitat, indicating a higher resource acquisition in the latter. When correcting for female size, fecundity was additionally increased in the invaded habitat through a significant decrease in egg size. This phenotypic response can be explained by differences in habitat structure between invaded and natural habitats: the former offers a more complex litter favoring nocturnal wanderers like *A. fulvolineata*. The existence of such an adaptive reproduction strategy depending on habitat suitability constitutes an original case of an invasion that favors an endangered species.

Keywords Biological invasion · Life history traits · Phenotypic plasticity · Rare species · Trade-off

Introduction

In response to variations in habitat properties, arthropods are known to exhibit phenotypic plasticity in several life history traits, such as dispersal behaviors (e.g., Bonte and Lens 2007), number and date of laying, and clutch size (e.g., Fox and Czesak 2000). Depending on the time of exposure to a presumed selection pressure, much of this

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plasticity is likely adaptive (Nussey et al. 2007). Reproductive output, as a component of fitness, depends on both the amount of resources acquired through a female's lifetime and the allocation of these resources between number of eggs and their volume (Smith and Fretwell 1974). In adverse conditions, theoretical as well as empirical approaches show an optimization of fitness by increasing size of eggs and decreasing number of eggs to improve progeny survival (e.g., Tamate and Maekawa 2000). However, few field studies have demonstrated how trade-offs differ among environmental conditions (Roff and Fairbairn 2007).

Although they represent a well-known threat for biodiversity (Cronk and Fuller 2001), biological invasions have recently been described as potential model systems for studying ecological processes as they modify both structure and functions of habitats (Sax et al. 2007). In Europe, many salt marshes have been recently invaded by the grass *Elymus athericus* (Bockelmann and Neuhaus 1999). Invaded habitats differ from natural ones (mainly dominated by *Atriplex portulacoides*, Chenopodiaceae) by their deeper litter (due to a lower rate of *Elymus* litter decomposition; Valéry et al. 2004) and by their taller plant cover, leading to important shifts in habitat structure and in associated arthropod communities (Pétillon et al. 2005a). As the spread of the invasion did not lead, at the moment, to the complete extinction of natural habitats, *E. athericus* created an interesting experimental design in which two contrasted habitats (natural vs. invaded) spatially and temporally coexist. These invasions thus provide opportunities for synchronically studying and comparing reproductive strategies between invaded and natural habitats for animal species that live in both habitats.

In the Mont Saint-Michel bay, such a case study can be found in the way that (1) *E. athericus* extended its area by threefold within only 10 years and now covers half of salt marsh areas (A. Radureau, personal communication) and (2) some species can be found in both habitat types, such as the dominant lycosid (wandering spider) *Arctosa fulvolineata*, a salt-marsh-restricted species (Roberts 1995). This species is fairly rare even within its habitat, and special conservation statuses are consequently assigned in several countries (e.g., classified as Nationally Endangered in the United Kingdom; Harvey et al. 2002). Like other wolf spider species, females carry their egg cocoon attached to the spinnerets at the end of the abdomen, which enables to accurately analyze the relation between female mass and individual reproductive traits.

In this study, we propose to examine if changes in salt marsh habitats due to plant invasion lead to changes in life history traits in this endangered spider. Recent studies show that population densities of *A. fulvolineata* were higher in invaded habitats (with densities more than ten times higher than in natural ones; Pétillon et al. 2005b), and we thus consider natural habitats as less suitable for *A. fulvolineata* than invaded ones. The following hypotheses were tested: (1) a lower reproductive success (considered here as a proxy of fitness and estimated by clutch mass) and (2) a higher egg size at the cost of a lower fecundity (as expected from the trade-off between egg size and number and empirically demonstrated in wolf spiders by Moya-Laraño 2002, Brown et al. 2003, and Hendrickx and Maelfait 2003) as larger eggs are expected to be favored under adverse conditions (e.g., Hendrickx et al. 2003a). We tested these hypotheses by comparing clutch mass, number, and volume of eggs between field-collected females from both natural and invaded salt marsh habitats.

Materials and methods

Study site and sampling stations

Spiders were collected in the Mont Saint-Michel bay, an extensive intertidal area (salt marshes and mud flats together cover 250 km^2) located between Brittany and Normandy (North West France). A couple of sampling stations (natural and invaded) were representative (large area and dominance by a single plant species) and distant enough to avoid exchanges of individuals between studied habitats. However, stations needed to be close to each other because comparing stations between different sites often lead to an increase of variance, by the existence of other co-varying factors (Oksanen 2001; main abiotic factors are not significantly different between habitats—Pétillon et al. 2005b). They also needed to be positioned at the same distance from the dike because of the existence of increasing soil salinity across the salt marsh, which strongly affects the distribution ranges and abundances of spider species (Pétillon et al. 2008), yet our model species occurs across the entire salinity gradient. Sampling stations were thus selected within the same site, separated by approximately 50 m and located 100 m from the dike (immerged once a month).

Field and laboratory data collection

Reproduction period ranges from April to August, with a single peak centered in May (J. Pétillon, unpublished data). To avoid samplings during a hypothetical second laying period, the presence of cocoon was regularly checked and samplings took place 2 weeks after the first observations of cocoons (i.e., before the minimal time necessary for a second reproduction, if exists, and during the reproduction peak). At mid-May 2007 (i.e., 2 weeks after the last flood event), 30 females of *A. fulvolineata* with their egg cocoon were hand collected in each habitat (invaded=dominated by

E. athericus and natural=dominated by *A. portulacoides*) in the Mont Saint-Michel Bay salt marshes (Vivier-sur-Mer site—48°60′N, 1°78′W, France). All individuals were kept in ethanol 70° until measurements.

In laboratory, female body dry mass (that globally indicates spider fitness and body condition when females just laid their cocoons, e.g., Jakob et al. 1996; Moya-Laraño et al. 2008), cocoon fresh mass, and cocoon silk mass were weighted to the nearest 0.1 mg. Clutch mass was calculated by removing silk mass from total cocoon mass. The number of eggs in each cocoon was counted and the length and width of ten, randomly sampled eggs per cocoon were measured to the nearest 0.01 mm. As eggs are ellipsoid in shape, egg volume was calculated according to the formula: egg volume=$\pi/6\times(\text{egg length})\times(\text{egg width})^2$.

Data analysis

Data were tested for normality prior to analysis by Kolmogorov–Smirnov test and $\ln(x+1)$ transformation was applied in case of non-normality (normality was then tested again). Since reproductive effort increases with female mass (e.g., Petersen 1950), comparisons of reproductive traits between habitats were also considered by adding the female mass effect in our models. Analyses of co-variance (ANCOVA) were performed using each reproductive trait (clutch mass, number of eggs, and egg volume) as dependent variable habitat as main factor and female mass as covariate (as recommended by García-Berthou 2001). Homogeneity of the slopes of dependent–covariate relationships was tested with the ANCOVA design that analyzed the covariate-by-factor interaction. 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). Results were expressed as mean ± S.E. Analyses were performed by means of the R software (Ihaka and Gentleman 1996; http://www.r-project.org/).

Results

Female dry mass and clutch fresh mass were higher in the invaded habitat than in the natural one (respective means for females=33.5±1.6 vs. 27.9±0.9 mg and for clutches= 111.5±5.0 and 81.6±4.2 mg). While a cocoon of a female living in an invaded habitat contained on average 147.7 (±6.4) eggs (mean volume=0.710±0.004 mm^3), this number was smaller in the natural habitat (103.8±5.7 eggs, mean volume=0.744±0.005). Female mass had a highly significant positive effect on both clutch mass and number of eggs, but had no effect on egg volume (Table 1; Fig. 1). Habitat suitability had a significant effect on the three reproductive traits of *A. fulvolineata* (Table 1).

Table 1 ANCOVA of the clutch mass/female mass, number of eggs/female mass and volume of eggs/female mass relationships in *Arctosa fulvolineata*

Variable tested	Source of variation	*F*	*df*	*P*
Clutch mass	Model 1 (test for interaction)			
	Female mass	193.3	(1,55)	<0.0005
	Habitat	92.8	(1,55)	<0.0005
	Female mass×habitat	4.0	(1,55)	0.051
	Model 2 (no interaction)			
	Female mass	186.3	(1,56)	<0.0005
	Habitat	88.1	(1,56)	<0.0005
Number of eggs	Model 1 (test for interaction)			
	Female mass	92.6	(1,56)	<0.0005
	Habitat	67.7	(1,56)	<0.0005
	Female mass×habitat	2.2	(1,56)	0.142
	Model 2 (no interaction)			
	Female mass	90.7	(1,57)	<0.0005
	Habitat	66.3	(1,57)	<0.0005
Volume of eggs	Model 1 (test for interaction)			
	Female mass	1.2	(1,55)	0.287
	Habitat	6.2	(1,55)	0.016
	Female mass×habitat	0.5	(1,55)	0.477
	Model 2 (no interaction)			
	Female mass	1.2	(1,56)	0.285
	Habitat	6.3	(1,56)	0.015

Habitat type is the dependent factor with two modalities (natural vs. invaded) and female mass is the covariate

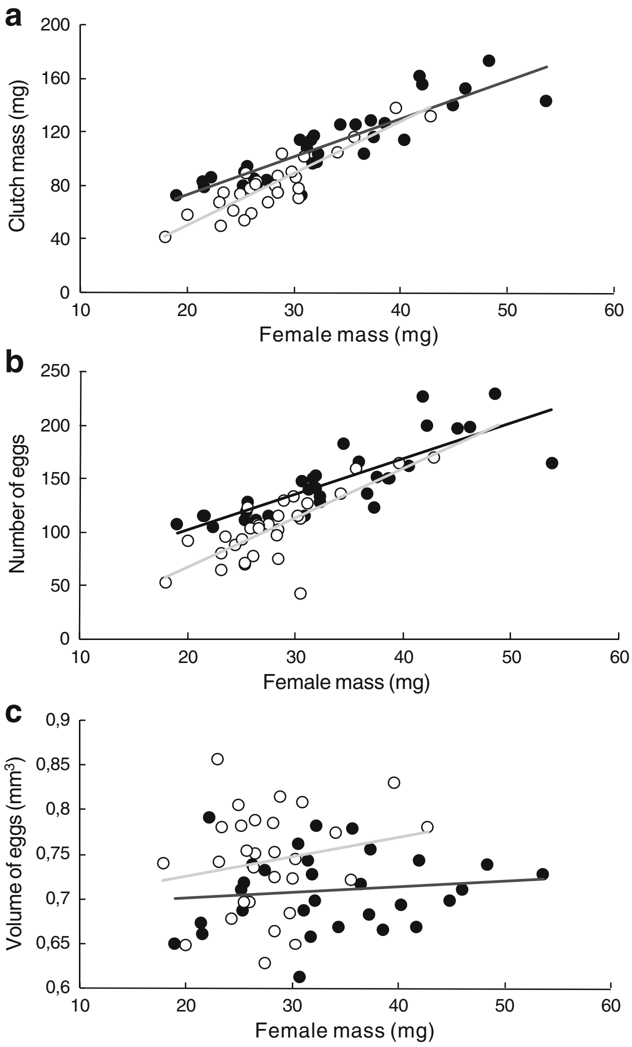

Fig. 1 Clutch mass (**a**), number of eggs (**b**), and volume of eggs (**c**) vs. dry female mass in *Arctosa fulvolineata*. *Filled and solid circles*: data from invaded and natural habitats respectively. *Black and gray lines*: linear regression in invaded and natural habitats respectively

Discussion

In this study, we show that mean female dry mass and reproduction output were significantly higher in invaded habitat than in natural one. Several factors like food resources, inter- and intraspecific competition, and habitat structure are likely to induce variations in these traits. Concerning potential prey of wandering spiders in salt marshes, a previous study showed that total densities of soil invertebrates are yet very high in both invaded and natural habitats (means ± S.E. as 26,293±3,707 and 60,352±7,053 individuals/m^2, respectively; Pétillon et al. 2005b), suggesting that food availability is unlikely to exert a limiting effect on *A. fulvolineata* female mass. Although the density of *A. fulvolineata* differs between natural and habitats, we would expect an opposite effect if intraspecific competition induces the observed effects. Higher intraspecific competition level would lead to an increase in development time and finally a decrease in body mass (e.g., Begon 1996) in invaded habitats. Species belonging to the trophic guild of *A. fulvolineata* (nocturnal wanderers) are found in the same densities in both natural and invaded habitats (Pétillon et al. 2005b), so there is no evidence for an increase in interspecific competition that can interfere in the use of food resources. As *A. fulvolineata* densities are very low (maximum of 1 individual/m^2 in invaded habitats) compared to habitat complexity (deep litter layer) and food availability (see above), we assume that intraspecific competition is too low for differently impacting female mass between habitat types. Finally, previous studies have emphasized the role of habitat structure in determining female size and reproductive output (e.g., Nilsen et al. 2004). In our case, *A. fulvolineata* might be favored by the structure of the invaded habitats: a deeper and more complex litter due to a lower rate of *Elymus* litter decomposition (Valéry et al. 2004). As a general rule, deep litter, by providing new microhabitats and more stable microclimate conditions (Wise 1993), notably tends to favor nocturnal wanderers (case of *A. fulvolineata*) (Bell et al. 2001). We thus suggest that *A. fulvolineata* prefers more heterogeneous litter of invaded areas, where it is often found during the day at 3–4 cm depth (J. Pétillon, unpublished data). Habitat structure consequently appears as the most important factor determining differences in female condition and related differences in cocoon mass between natural and invaded habitats. Nevertheless, it must be stressed that rates of predation and densities *per se* can also act directly on fitness (Heath et al. 2003; Berec et al. 2006) and should thus be investigated further.

The present study showed the existence of an adaptive reproduction strategy depending on habitat suitability, leading to an increase in egg size in unsuitable conditions. Eggs were larger, presumably reflecting a higher content in lipids (Anderson 1990; Moya-Laraño et al. 2008) but in lower numbers to increase offspring fitness in unfavorable habitats, whereas in favorable habitats, eggs were smaller but more numerous to increase female fecundity. Some studies already showed a trade-off between number and size of eggs (for spiders, see Spence et al. 1996; Brown et al. 2003; Hendrickx and Maelfait 2003), but this trade-off can be hard to detect due to its interference with differences in resource acquisition among populations or individuals (van Noordwijk and de Jong 1986; Walker et al. 2003). A reduced reproductive output can be compensated by increasing offspring size, this strategy being predicted to maximize parental fitness (Hendrickx et al. 2003b). Although previous studies on egg size differences among populations of wolf spiders showed that egg size can be strongly genetically based (Hendrickx et al. 2008), the close distance between both populations renders rather unlikely that this divergence is genetically based in our study system. Phenotypic plasticity is in general adaptive to variations in both mother and environmental factors (respectively Carter et al. 2004; Lardies and Bozinovic 2008). Here, changes in habitat structure due to the invasion can be considered as a presumed selection pressure and we assume that the observed differences in reproductive outputs and life history tactics can be explained by phenotypic plasticity in female mass and resource allocations, respectively. Nevertheless, the question of genetically driven plasticity in reproductive traits cannot be unequivocally excluded. As gene flow can be strongly reduced between populations after only dozens of generations (due to divergence in phenotypic traits; Hendry et al. 2007), then invasions would be old enough for leading to an isolation of populations (around 15 generations of spiders were in contact with the invaded habitat). This hypothesis can only be tested by an experiment of habitat permutation or/and quantitative genetic approach, especially for testing the existence of possible adaptive genetic change.

Our study finally constitutes a unique example of an invasion that favors a rare species and proves the role of biological invasions as an emerging insight for studying ecological and evolutionary processes (Sax et al. 2007).

Acknowledgments We are indebted to Yann Cozic and William Montaigne for help during field collection. Alain Radureau kindly provided some data on salt marsh vegetation. Luc Lens, Frederik Hendrickx, and two anonymous referees provided very useful comments on earlier drafts. The first author holds a visiting post-doctoral fellowship from the Fund for Scientific Research—Flanders (FWO-project G.0202.06).

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