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ORIGINAL PAPER

Cross-habitat variation in the phenology of a colonial spider: insights from a reciprocal transplant study

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Abstract In species with widespread distribution, populations found in markedly different environments can show differences in developmental traits. This, in time, can have an effect on reproductive success. Sources of variation in developmental traits can be genetic or environmentally induced. I examined the relationship between environmental and genetic influences on juvenile development in populations of the colonial spider, *Parawixia bistriata*, located at sites with different moisture regimes and associated environmental variables (e.g., prey availability). It was expected that individuals from different populations would show differences in developmental traits and that those differences will be associated with lower reproductive success at dry sites. I recorded the phenology and developmental traits of native and transplanted individuals in the field and estimated reproductive success based on clutch size. Colonies from wet versus dry sites showed different phenologies, with individuals at dry sites maturing later. Transplant results suggest plasticity in instar duration caused by environmental effects. Despite differences in resources and spider phenology, clutch sizes of native dry and wet populations were similar. Transplanted individuals, however, were differentially affected. Transplants from wet to dry sites (WD) showed lower growth rates and smaller clutches, whereas transplants from dry to wet sites had larger clutch sizes than in native habitat. Delayed maturation and failure to reproduce in WD individuals is associated with a lower tendency to capture prey in groups and less aggressive interactions during prey capture. Thus, despite negative environmental effects on development, dry native individuals have evolved non-developmental traits that allow successful reproduction.

Keywords Developmental pattern · Clutch size · Plasticity · Ecotypic variation · *Parawixia bistriata*

Introduction

Widespread species are likely to experience diversity of environmental conditions and to exhibit differences in life history traits in response to this variation. Environmental factors such as resource levels have an effect on developmental rate, phenology, and reproduction. Less productive environments, especially those with a definite growing season, are associated with slower developmental rates, smaller adult size, and smaller clutch sizes (Hassall et al. 2003, 2005; Uhl et al. 2004).

In organisms like insects and spiders, fitness is strongly influenced by developmental traits such as instar duration, number of molts, and the size increment associated with ecdysis (Higgins and Rankin 1996). In turn, these traits affect the timing of reproduction and the number of offspring produced by determining age and size at maturity. These developmental traits may respond to environmental variation, and they may thus be subject to change as a result of selection pressure.

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The sources of variation in life history traits within a species can be genetic or environmentally induced. To distinguish between these two factors, one can compare reaction norms (the set of phenotypes expressed by a genotype across environments) for the traits involved (Stearns and Koella 1986; Carroll and Corneli 1999). Both common garden experiments and reciprocal transplant studies allow examination of reaction norms for traits that might show population divergence. An advantage of reciprocal transplants, however, is the possibility of testing for local adaptation and to distinguish between genetic and environmental effects under a natural setting. Only recently have reciprocal transplant experiments become a common practice to disentangle causes of geographic variation in phenotypes, especially in arthropods (Crozier 2004; Fordyce 2003; Riechert and Hall 2000; Arnett and Gotelli 1999).

In spiders, there is a close correspondence between foraging rate, growth, and fecundity. This makes them a good model for the study of the effect of the environmental conditions on development and reproduction. Moreover, the foraging rate of a spider is not only determined by the rate of encounter with prey but also by body temperature, which is itself a function of the physical environment (Riechert and Tracy 1975) as well as by individuals' aggression levels that affect the tendency to attack prey and can have a genetic basis (Arnqvist and Henriksson 1997). Thus, differences in the biotic and abiotic environment and genetic factors that affect foraging behavior are reflected in the development and reproduction of individuals.

The effect of variability in food resources on the development of spiders has been shown in manipulative studies. Spiders may respond to experimentally induced changes in prey levels by modifying the number of molts and maturing later at a similar size (Miyashita 1968; Higgins 1992, 1993; Mayntz et al. 2003) or smaller size (Miyashita 1968; Higgins 1992, 1993) than under natural conditions, or alternatively, by maturing after the same number of molts but at a smaller size (Mayntz et al. 2003). Thus, species or even sexes within a species may show different developmental responses to changes in resources. In addition, food resources may also affect body condition (relative amount of energy reserves), as shown in manipulative studies (e.g., Uetz et al. 2002; Fernández-Montraveta and Moya-Laraño 2007; Moya-Laraño et al. 2008).

In this study, I examine life history trait variation in a widely distributed, colonial South American spider, *Parawixia bistriata* (Araneidae). I studied populations located at the same latitude (26°S) but with different seasonal constraints in the Chaco region of Argentina (Fig. 1). Although both habitat types exhibit dry and wet seasons, the duration and strength of the dry season is less severe in the wet habitat type. Spider colonies in the dry site are thus expected to experience lower prey levels and to exhibit different developmental pathways in response to variations in habitat conditions. Colony censuses were completed to examine if differences in colony phenology exist between habitats. Reciprocal transplants were performed to examine the mechanisms underlying the observed differences in population responses to environmental variation and examined two developmental traits (size at ecdysis and instar duration) to determine whether plasticity in any of these traits could explain the different phenologies. I also recorded body condition and clutch size as an estimation of fitness of individuals in the different populations. Due to lower resources in the dry sites, native individuals are expected to be negatively affected by them showing differences in developmental traits such as lower growth rate, less change of size at ecdysis, lower body condition, and smaller clutch sizes. If these differences are exclusively caused by environmental forces, both native

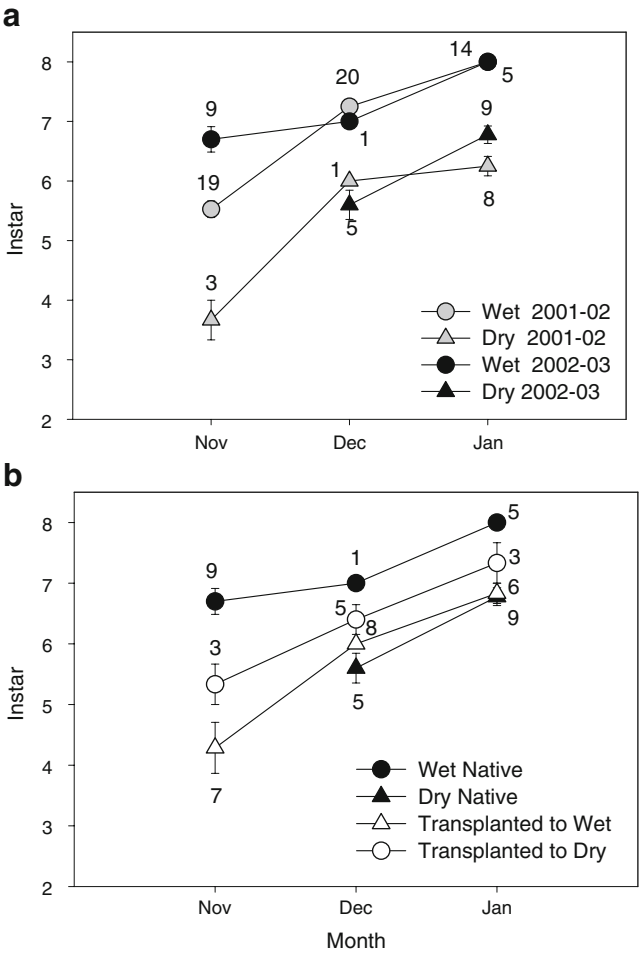

Fig. 1 Developmental pattern of native and transplanted colonies of *Parawixia bistriata*. **a** Developmental pattern of native colonies during the study period November 2001–January 2002 and November 2002–January 2003. **b** Developmental pattern of native and transplanted colonies in wet and dry habitats during the season November 2002–January 2003. *Numbers next to symbols* are the number of colonies sampled during a month. *Error bars* indicate standard errors

and transplanted individuals located in the low prey environment are expected to show a lower growth rate and clutch size than individuals in wet sites with more prey and milder seasonality regardless of their habitat of origin. If genetic forces are responsible for inter-population differences, transplanted individuals should exhibit a development similar to the native individuals in their habitat of origin.

Methods

P. bistriata

P. bistriata colonies are comprised of a communal retreat and thread framework built by sibs. Spiders stay in the retreat during the day and move out onto the thread framework each night to build individual orb capture webs. The orb webs are consumed each day as the individual spider moves back into the central retreat.

Though this univoltine spider is typically found in dry forests, it is common in a diverse range of habitats from semi-arid scrub to wet forests in southeastern South America as the Chaco region in Argentina, Bolivia, and Paraguay, and the Cerrado in Brazil (Levi 1992). Sandoval (1987) has studied the life cycle of *P. bistriata* in the Brazilian Cerrado, a mosaic of dry forest and savanna extending between 6° to 23° latitude. She reported that the life cycle consists of eight instars in both sexes with juveniles reaching the sixth instar and subadult and adults as seventh and eighth instars, respectively. Adults are found in the austral fall, produce egg sacs at that time, and die soon after oviposition. While the spiderlings actually hatch during the winter, they remain in the egg sac until spring when each clutch forms a new colony consisting of second instar sibs (the spiderlings undergo one molt within the egg sac) and have a second molt soon after emergence from the sac. Individuals within a colony molt synchronously within a few days of one another (Fowler and Gobbi 1988) and the cohort remains aggregated in the colony until completion of the seventh molt when both male and females mature. At this time, females leave the nest to initiate egg laying in isolation. Mating can occur either before dispersal when mature individuals are still aggregated (Fernández Campón, personal observation) or after dispersal when individuals are solitary (Sandoval 1987).

Study sites

All study areas were situated in the Chaco region of northeastern Argentina (26°) where precipitation decreases and seasonality increases from east to west (Cabrera 1971). Thus, despite the fact that the entire region has dry winters and wet summers, the level and temporal variability in precipitation differ between respective dry and wet study sites. There are corresponding differences, in the species composition of the vegetation, in vegetation structure and also expected differences in insect abundances.

I established a pair of sites in eastern Wet Chaco (termed "wet sites") and another pair of sites 400 km to the west in a transition area between Wet and Semiarid Chaco (termed "dry sites"). The two wet sites were situated 80 km apart in the Formosa province of Argentina, Wet 1 at a provincial reserve, Guaycolec (26°10′S, 58°12′W, 60 m a.s.l.), and Wet 2 at a private reserve, El Bagual (26°10′S, 58°56′W, 75 m a.s.l.). The dry sites were located close to the town of Pampa del Infierno (26°30′S, 61°10′W, 120 m a.s.l.) in the Chaco province, Dry 1 on the Allende family ranch 7 km northeast of the town and Dry 2 on a railroad right of way on the eastern side of the town on public-owned land (due to human disturbance, it was not possible to complete experimental manipulations at the site Dry 2. Thus, this site only provided data on the developmental pattern of native colonies).

I assumed that *P. bistriata* located at each site represented a distinct population and, thus, considered the two replicates for each region as independent samples within the respective habitat type. This assumption was based on: (1) the noted low vagility of adult spiders (adults traveled distances of only 200–500 m when dispersing from the colony at reproduction; J. Kochalka personal communication; Fernández Campón personal observation), (2) the patchy distribution of colonies, and (3) the distance between study areas relative to vagility of individuals.

Climatograms describing the temperature and precipitation patterns of dry and wet sites are shown in supplementary material S1. Both habitat types have a marked dry season in the winter and wet summers during which 80% to 90% of the annual precipitation occurs. While the daily mean temperature regime is similar between habitat types, freezing days are more frequent and annual precipitation lower in the dry sites (supplementary material S2).

Insect biomass

Malaise traps (Bioquip model #2875AG) were used to quantify insect biomass in wet and dry habitats. Although this is not an exact measure of what spiders can consume at each site (Castillo and Eberhard 1983), it is an estimate of the potential prey population available to spiders. Insect biomass data were collected over three sampling periods for each site during the field season extending from October 2002 to January 2003. Two Malaise traps, located 10 m apart, were set at each site. After each sampling period, I moved on to a different study area and thus censused sites sequentially in the order Wet 1, Wet 2, and Dry 1 throughout the field season. Insect samples were collected between 1930–0700 hours coinciding with the activity

period of *P. bistriata*. No samples were collected on rainy nights; thus, the potential eight-night sampling period varied from 2 to 8 days.

Insects collected in each trap for each trap night were preserved in individual vials with 70% ethanol and were taken back to the laboratory to be oven-dried for weight estimation. They were then placed in a drying oven for 20 h at 66°C. Dried samples were weighed to 0.001 g using a Mettler electronic balance.

Transplants

Reciprocal transplants of spider colonies were performed between habitats to identify genetic and environmental sources of variation in life history traits between populations from dry and wet habitats. No transplants were made within the immediate vicinity of existing colonies (minimum distance to native colony was 200 m). At each locality, transplanted colonies were placed in pairs at 20-m distances along the forest edge. In pairing the transplants, I hoped to increase the probability of successful establishment in the novel environment. A detailed description of the transplants protocol is described in (Fernández Campón 2005).

All transplanted individuals were at the same developmental stage (third and fourth instars). Due to differences in the phenologies of dry and wet populations (see "Results"), colonies were transplanted at different times of the year. During the second year of the study, on 15 June 2002, I transplanted ten colonies collected in Formosa city (25 km south and 70 km northeast from Wet 1 and Wet 2, respectively) to the site Dry 1 (wet to dry (WD) colonies). Of these, five colonies were successfully established after having over-wintered in the dry site for a period of 4 months. The transplant of dry colonies to wet sites was completed on October 8, 2002 using colonies collected from a site located in the vicinity of Dry 1. Of the ten colonies transplanted at the two wet sites (dry to wet (DW) colonies), three colonies were relocated at Wet 1 and five colonies at Wet 2.

Phenology and developmental traits

In order to assess spider development, native colonies were sampled over two field seasons from October to January, 2001–2002 (N_{dry}=13; N_{wet}=53) and 2002–2003 (N_{dry}=14; N_{wet}=15). Transplanted colonies were sampled during the second season from October to January 2002–2003 (N_{WD}=5; N_{DW}=8). These periods correspond to mid spring to late summer in the Southern Hemisphere, which is the rainy season in the Chaco. At each census, sampled colonies were chosen haphazardly at a site.

Instars of *P. bistriata* are easily recognized by their color pattern. During immature instars, individuals of *P. bistriata* present a distinct coloration characterized by a black background and red lateral bands. As these spiders approach the penultimate instar, the red lateral bands become red dots and white lines appear. Once they molt to adults, there is a remarkable change in coloration, particularly in females. Adults present sexual dimorphism in body size as well as coloration. Males resemble the pattern of coloration of penultimates but with a brown background, whereas females, with a more developed opisthosoma, are yellow or brown. Individuals within a colony molt in synchrony within a few days (Fowler and Gobbi 1988). If at the time of the census there were individuals of two consecutive instars, those individuals of an earlier instar would molt to the next instar within a few days. Thus, I classified colony developmental stage (instar) as that of individuals of the ultimate instar within the colony. In order to validate the method of classification of the developmental stage of colonies, a number of colonies ("validation colonies") from the two habitats types were collected and dissected (N_{dry}=7, N_{wet}=16). In each validation colony, all individuals were counted, sexed, and weighed as described below.

To examine the developmental traits of individuals within colonies in the field, I performed a census every 30–40 days. At each census, between five and ten individuals from each colony were haphazardly collected to estimate growth rate and change in size at ecdysis. Each individual spider was weighed to the 0.001 g using a field scale (Acculab model #PP-2060D, Sartorius group), and its cephalothorax width and body length were measured to the 0.01 mm using digital calipers. Because the cephalothorax is a hard part of the exoskeleton, it is a good indicator of an individual's growth during each molt. Spider mass is more indicative of foraging success within each instar and was used as an estimate of growth rate for comparisons among treatments groups. Body condition was calculated as the residuals of the regression of the natural logarithm of mass against natural logarithm of body length (Uetz et al. 2002).

After measurements were taken, individuals were returned to their respective colonies. For the growth rate estimates, juveniles, adult, and subadult females were sampled. Sandoval (1987) showed that patterns of growth differ between sexes at those developmental stages. To examine the change in size at ecdysis and body condition, I used data on fifth and sixth instar individuals because these were the developmental stages present in the four treatment groups (native and transplanted individuals in both habitat types) during the study period.

Clutch size

Females produce a single egg sac in the field and died shortly thereafter (with the exception of a single female that

produced three egg sacs). Thus, the clutch size of the single egg sac is a good estimate of female lifetime fecundity. Egg sacs produced by native and transplanted individuals were collected in the field between February 24th and May 12th and maintained in the laboratory until hatching. Because native individuals from dry and wet populations have different phenology, they produced egg sacs at different times of the year (W: January–February, D: April–May), transplanted individuals produced egg sacs in between (DW: early April; WD: late March). To calculate the total number of eggs produced per sac, I counted spiderlings at hatching and unhatched eggs. Spiderlings were later returned to their mother's site of origin. All the egg sacs produced by females from transplanted colonies that were found in the field were collected. It is possible to differentiate egg sacs produced by native and transplanted females at each site on the basis of proximity to existing colonies and the appearance of the casing of the egg sacs. Egg sacs produced by females of wet habitat of origin are yellow; those produced by females of dry habitat of origin has an extra layer of white silk. This extra layer seems to serve as protection overwintering within the egg sac against desiccation during the cold dry winters in the dry sites (Fernández Campón, unpublished).

Colony size

Colony size was estimated by counting the number of individuals on the webs and the retreat during the nocturnal activity period. This is a non-destructive and effective way to census colonies as this species is active at night, and most of the individuals of a colony are outside the retreat on their capture webs during the nocturnal foraging period. Only colonies with sixth instar individuals were sampled. Colony size of seven colonies located at the site Wet 1 was estimated by two observers. To assess the degree of inter-observer reliability in colony size estimation, I performed a Spearman correlation (Spearman's rho=0.93, N=7, P=0.01). Subsequent estimations of colony size were performed by one or the other of these two observers.

Data analysis

I used a repeated measure analysis of variance (ANOVA) to test for habitat and temporal differences in insect biomass between habitats. Habitat type (wet or dry) was used as the independent variable between subjects (traps), and the variable time (corresponding to the three sampling periods) was the within-subject independent variable. Insect biomass per trap night (dry weight in grams) was the dependent variable.

Data on the phenologies of native individuals from dry and wet sites consisted of small integer counts, which violated the assumptions of parametric statistical tests. I applied a generalized linear model with Poisson errors, a log link function, and type III significance tests (Poisson regression) to these data using the PROC GENMOD of SAS version 8 (Stokes et al. 2000). Examination of the diagnostics (i.e., deviance and *df*) indicated that the data were under-dispersed. The data were thus scaled using the deviance to improve the fit to the model (Stokes et al. 2000). In this case, the type III analysis is based on the F probability distribution instead of χ^2 distribution. The selected model was the one that presented the best fit to the data using a likelihood-based χ^2 test (Stokes et al. 2000). Variables or interaction terms that were not significant were excluded from the model. In the Poisson regression model, the variables habitat (wet versus dry), year (field season 1 versus 2), and day (continuous variable that identifies the day within a field season) were the explanatory variables. The developmental stage of a colony (instar) was the response variable. To assign values to the variable day, the first day of the study period was assigned the number 1, and subsequent days were numbered. (Note that in the graphical representation of these results, monthly averages are shown for ease of interpretation).

I performed a general linear model similar to the one described above to compare the phenologies of native versus transplanted individuals. In this new model, the variables origin (habitat of origin), rearing environment (habitat type where colonies had developed), and day (defined as in the previous model) were the explanatory variables. Again, the developmental stage of a colony (instar) was the response variable. I used the sequential Bonferroni correction (Rice 1989) to determine which groups were causing the significant interaction effects in the analysis.

The change in spider mass with time was used as an estimate of growth rate. The variable spider mass was log transformed to linearize its relationship with the variable days. I applied a general linear mixed model (GLMM) to the growth rate data. Data on individuals of wet and dry origin were analyzed separately. The GLMM included the variables day and habitat (native or transplanted) and the interaction day×habitat as fixed factors and site nested within habitat as a random factor. I performed a GLMM to compare the change of size at ecdysis (cephalothorax width) and body condition between native and transplanted individuals of both dry and wet habitat of origin. The model included the variables origin, rearing environment, and instar as the fixed factors and site nested within rearing environment as the random factor.

Clutch size and the size of native colony data did not meet normality assumptions; thus, the rank of these data was used as dependent variables in analyses of individual and colony success (Conover and Iman 1981). The GLMM

for clutch size included the variable site nested within rearing environment as a random factor. Fixed factors in this model were the presence or absence of egg sac parasitoids, rearing environment, and habitat of origin of spiders (as described above). The size of native colonies was also analyzed using a GLMM, with habitat as the independent variable and site nested within habitat as a random factor.

Results

Insect biomass

Insect biomass differed between habitat types (repeated measures ANOVA $F_{1,\ 6}=16.29$, $P<0.001$; supplementary material S3). Overall insect biomass was higher in the wet sites than in the dry site (mean±SE (gram): $Dry_1=0.16\pm 0.02$; $Wet_{1+2}=0.28\pm 0.04$; supplementary material S4).

Spider phenotypic traits

Table 1 shows a summary of the main results on spider phenotypic traits described below.

Phenologies

Validation colonies were comprised primarily of two instars: 57% of the ultimate instar and 41% of the penultimate instar. These results support the method used for classifying the developmental stage of a colony by the ultimate instars. In those colonies comprised of individuals of three different instars, individuals of the antepenultimate instar constituted only between 2% and 4% of the colony. The proportion of colonies containing individuals of three different instars was larger in the dry sites (0.71) than in the wet sites (0.19; $\chi^2=5.96$, $df=1$, $P=0.01$). When colony size is considered, colonies with individuals of three instars were larger than those colonies with individuals of one or two instars (Logistic regression; colony size: $\chi^2=5.08$, $df=1$, $P=0.02$). Colony size and rear environment showed a significant interaction in the probability of finding a colony with individuals of three different instars (rear environment×colony size: $\chi^2=4.26$, $df=1$, $P=0.04$), suggesting that the effect of colony size varies with the rearing environment. Rearing environment was not statistically significant ($\chi^2=3.58$, $df=1$, $P=0.06$).

Native colonies Colonies in dry versus wet sites were at different developmental stage at any sampling period during the study (Table 2). These differences were consistent between years (interaction year×rearing environment was not significant and was excluded from the final model) despite an overall inter-annual variability at both sites (significant effect of the variable year). At any particular census month, there was an average difference of two instars in the developmental stage of colonies from wet sites (more advanced stage) and the dry site (Fig. 1a). By the time wet individuals reached adulthood, individuals from dry populations were in the sixth instars, two molts from the adult stage. In addition, there were differences in the developmental rates observed between colonies in the two habitat types sampled during the 2 years (significant three-way interaction).

Table 1 Summary of results

Phenotypic traits	Native individuals	Transplants	Source of variation
Phenology	Different in dry and wet native populations (Table 2, Fig. 1a)	It is delayed when individuals are transplanted from wet to dry habitat (Table 3, Fig. 1b)	Variable (environmental effect)
Growth rate (change in mass with time)		Decreases when individuals are transplanted from wet to dry habitat. Differences are not significant among individuals of dry origin (supplementary material S6)	Variable (environmental effect on instar duration)
Change of size at ecdysis[a]	Differences found among fifth instar individuals. Differences disappear in sixth instar and subadult individuals	No effect of rearing environment (Table 3) Seems to be a canalized trait	Canalized trait
Body condition[b]		Fifth instar individuals show both origin and rearing environment effects; sixth instar individuals show only environmental effects (Table 3)	Variable (environmental effect)
Lifetime reproductive success[c]	Similar among dry and wet natives (Fig. 2)	Rearing environment negatively affects wet origin individuals (Fig. 2)	Variable (environmental and genetic effects)

[a] Estimated as cephalothorax width at different instars. See the text for an explanation

[b] Estimated as residuals of the regression Lnmass×LnBL by instar (Uetz et al. 2002)

[c] Estimated as clutch size. See the text for an explanation

Table 2 Generalized linear model analysis of the developmental stage of native colonies in both habitats during the two field seasons and of native and transplanted colonies in both habitats during the second season (Poisson errors, log link)

Population	Source	Degrees of freedom	F	P	χ^2	P
Natives (two seasons)	Day	1, 114	142.64	<0.001	142.64	<0.001
	Rearing environment	1, 65	7.06	0.01	7.06	0.01
	Year	1, 114	16.22	<0.001	16.22	<0.001
	Rearing environment×year×day	3, 114	13.01	0.01	13.01	<0.001
Native versus transplants	Day	1, 65	124.11	<0.001	124.11	<0.001
	Rearing environment	1, 65	7.06	0.01	7.06	0.01
	Origin	1, 65	30.26	<0.001	30.26	<0.001
	Rearing environment×origin	1, 65	6.08	0.02	6.08	0.01
	Origin×day	1, 65	9.07	<0.001	9.07	<0.001

Natives, two seasons: deviance=6.59; *df*=114; native versus transplants: deviance=3.64; *df*=65

Native and transplanted colonies Native and transplanted colonies at both dry and wet sites showed differences in their developmental stage (Table 3). Transplants developmental stage was intermediate between that of natives at any time during the study period. Developmental rate seems to be accelerated when transplanted to wet sites and decreases when individuals are transplanted to dry sites compared to development in their native habitat (Fig. 1b). Overall, developmental stage was more advanced at wet sites with colonies composed on average of later instars over the course of the season (significant rearing environment effect). Likewise, native and transplanted colonies of wet origin (W and WD) are developmentally more advanced than natives and transplants of dry habitat origin (D and DW; significant origin effect in the model). There were also two significant interaction effects: between rearing environment and origin and between origin and day (Table 3). The significant interaction between rearing environment and origin indicates that the two classes of transplants exhibited different developmental responses. I completed contrasts to further delineate these differences (supplementary material S5). The significant contrast effect reflects the fact that WD transplants showed delayed development compared to the W natives (Fig. 1b).

Developmental traits

Growth rates of D natives and DW transplants (represented in the model by the interaction rearing environment×day) was similar ($F_{1,200}$=0.00; P=0.99; supplementary material S6). However, the growth rate of W natives was higher than that of WD transplants ($F_{1,231}$=9.21; P<0.001; supplementary material S6). Differences in the average mass of spiders during the time following transplantation and beginning of data collection were reflected in the significant effect of rearing environment in this analysis.

Change of size at ecdysis, measured as cephalothorax width (CW), differed between instars and between individuals

Table 3 General linear mixed model of cephalothorax width (CW) and body condition (BC; residuals Ln(mass)×Ln (body length) regression) of fifth and sixth instar individuals native and transplanted individuals of dry and wet origin

Trait	Source	Degrees of freedom	*F*	*P*
CW	Instar	1, 182	141.21	<0.001
	Rearing environment	1, 1.42	<0.001	0.99
	Origin	1, 222	4.89	0.03
	Rearing environment×origin	1, 222	0.62	0.43
	Instar×rearing environment	1, 224	1.22	0.27
	Instar×origin	1, 182	8.97	<0.001
	Rearing environment×origin×instar	1, 224	0.55	0.46
BC	Instar	1, 72.7	0.13	0.72
	Rearing environment	1, 28.9	12.14	<0.001
	Origin	1, 28.9	20.75	<0.001
	Rearing environment×origin	1, 28.9	0.30	0.60
	Instar×rearing environment	1, 72.7	0.79	0.38
	Instar×origin	1, 72.7	7.73	0.01
	Rearing environment×origin×instar	1, 72.7	0.53	0.47

Covariance parameter estimates. CW: site (rearing environment)= 0.01; residual=0.04; BC: colony (site)=0.00; residual=0.01

of dry and wet habitat origin (Table 3; supplementary material S7). However, rearing environment was not a significant effect in the model, implying that CW is not a plastic trait. Multiple comparisons indicated that differences in CW among individuals from dry and wet origin occurred among fifth instar individuals (t=3.94, df=223, P<0.001) but not among sixth instar individuals (t_{224}=−0.55, P=0.95).

CW of subadult natives (seventh instar) of dry and wet populations was similar ($F_{1,1}$=13.80; P=0.17; N=108). Assuming CW will not show plasticity when individuals molt to the adult stage, this will indicate that native individuals from dry and wet habitats mature at the same size.

Body condition showed differences between individuals from wet and dry site of origin and between rearing environments (Table 3). Individuals from wet habitat of origin (W and WD) had more reserves, and the same happened with those individuals found in wet sites being native or transplanted (W and DW). The significant interaction between instar and origin indicates that whole individuals of dry origin (D and DW) increase their energetic reserves during development (from fifth to sixth instars); individuals from wet origin decrease their reserves. Multiple comparison analysis showed that there were no significant differences among the four treatment groups when individuals are in their sixth instar.

Clutch size and colony size

Some of the egg sacs collected in the field had been parasitized (supplementary material S8). The incidence of parasitism in the egg sacs collected was similar among groups (G_2=4.95, P>0.05; WD was not included in the analyses due to the small number of egg sacs found, N=2). The number of unhatched eggs and spiderlings in parasitized egg sacs could be counted in all egg sacs except for two sacs produced by WD individuals. In these sacs, the egg mass was decomposed such that individual eggs could not be counted. The presence of parasitoids did not affect number of eggs produced per sac ($F_{1,\ 57}$=2.15, P=0.15). Although a significant three-way interaction effect was noted (supplementary material S9), multiple comparison analysis indicated that the only significant difference in the number of eggs was between parasitized sacs produced by DW individuals and the non-parasitized sacs produced by WD individuals (t_{57}=3.27, P=0.03). Because no significant differences in the number of eggs per parasitized and unparasitized sacs were observed within treatments groups, it was possible to pool parasitized and unparasitized egg sacs in the examination of the effect of the rearing environment and habitat of origin.

Clutch sizes of individuals reared in wet sites (W and DW) were significantly larger than noted in the dry habitat ($F_{1,\ 57}$=7.01, P=0.01; Fig. 2). There was also a habitat of origin effect but no significant interaction between rearing environment and habitat of origin (supplementary material S9). The significant effect of habitat of origin indicates that sacs produced by individuals originating in the dry habitat (D and DW) had more eggs than sacs produced by individuals of wet habitat of origin (Fig. 2). Multiple comparison analysis indicated that clutch sizes produced by native individuals in both habitats was similar (D versus W: t_{57}=1.06, P=0.29). Conversely, within wet habitats, the number of eggs in sacs produced by transplanted individuals was significantly larger than native individuals (DW versus W: t_{57}=2.86, P<0.001) and was also larger than those produced by native individuals in the dry habitat (D versus DW: t_{57}=−2.28, P=0.026, critical value$_{\text{seq Bonferroni}}$=0.025). Statistical comparisons of sacs produced by WD individuals were not possible due to the small sample size (N=2). The number of eggs in these two sacs was at the lower end of the spectrum noted for the other treatment groups (Fig. 2).

Native colonies were larger in dry versus wet sites ($F_{2,\ 51}$= 114.39, P<0.001). Average colony size in the dry sites was twice the size of colonies in the wet sites (supplementary material S10).

Discussion

In this study, I examined whether populations under different environments showed different developmental pattern and whether this was reflected in the reproductive success of individuals in dry and wet environments. In addition, I examined whether differences in developmental pattern had a genetic basis or were environmentally induced.

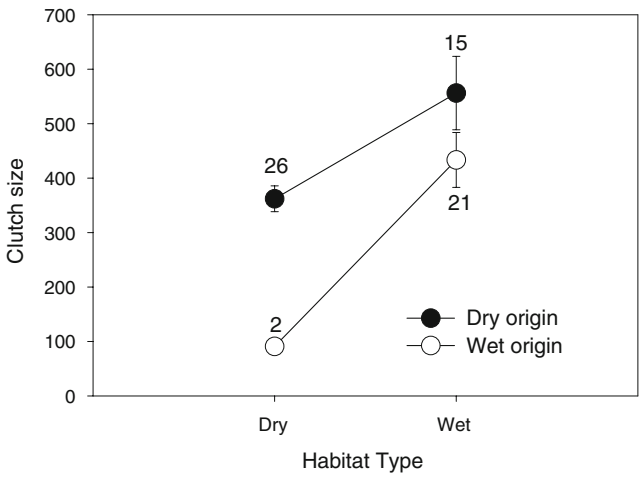

Fig. 2 Clutch size (number of eggs per sac) of native and transplanted individuals in both habitats. *Numbers over circles* indicate sample sizes; *error bars* indicate standard errors

Phenologies of native populations in dry and wet sites were out of phase. In January, when adults from wet populations are found in the field, spiders in the dry sites are in their sixth instar (adult individuals appear in early fall in March, Fernández Campón peronal observation). Comparison of the developmental pattern of native and transplanted individuals suggested that while some traits such as instar duration are plastic and can be induced by environmental conditions, others such as change in size at ecdysis did not vary and seem environmentally canalized (Debat and David 2001).

Differences in phenologies seemed to be caused by environmental factors affecting instar duration as suggested by the change in the developmental rate of WD individuals. Native individuals in wet sites (W) molted three times during the 5 months that elapsed between transplantation and the start of the data collection when they were in the seventh instar. On the other hand, most individuals from colonies transplanted to the dry site (WD) were still in the fifth instar and molted only once during those 4 months (Fig. 1b). Failure to find differences in the developmental rate of native and transplanted individuals of dry habitat of origin (D and DW) could be attributed to the short duration of time the transplanted individuals had been in the novel environment previously to being sampled (1 month) rather than to the possibility that the instar duration is a fixed character in individuals of dry habitat origin. The fact that CW did not show differences among groups of the same habitat of origin despite differences in rearing environment suggests that change in the size at ecdysis is a canalized character. Individuals need to reach a certain threshold size or critical weight (Davidowitz and Nijhout 2004) before they can molt. Results agree with what was found for *Manduca sexta* (Lepidoptera) for which instar duration is a plastic trait responding to changes in temperature, whereas the critical weight was found to be a fixed trait under different temperature conditions (Berner and Blanckenhorn 2007).

The existence of a threshold size for molting could be a constraint to maturation before the end of the growing season. Late maturing spiders would encounter two problems: (1) during the adult stage, they would have difficulty reaching energy requirements for oviposition, or (2) there may not be surviving males (Henschel et al. 1995). If the number of molts is a plastic trait, individuals under low resources would mature before the growing season ends but after less molts and having achieved a smaller size. This incurs a cost of lower fecundity (Higgins and Rankin 1996; Higgins 2000). Although I did not measure adult size, cephalothorax width was similar in subadult natives of both habitat types suggesting that until that stage, individuals mature at the same size. In addition, I did not find evidence of a decrease in fecundity in native individuals in the dry sites compared to native individuals in the wet sites.

P. bistriata seems to have a fixed number of molts and a threshold size for molting (fixed size at ecdysis). This developmental pattern can be particularly important constraint for individuals under low resources and a more severe dry season (Higgins and Rankin 1996). It is possible that a fixed size at ecdysis is constraining the life cycle of individuals in the dry habitat type and that not all individuals mature in time to reproduce before the end of the wet season (there was a higher proportion of colonies comprised of individuals of three different instars at dry sites). If that is the case, as judged by the clutch sizes and the size of colonies, those individuals that do get to reproduce in the dry sites seem to have been able to overcome constraints imposed by seasonality and developmental pattern. From this, it follows that developmental traits are not causing the differences in fecundity of native individuals in dry and wet populations.

Disturbance caused by manipulating the colonies during transplantation could be discarded. Although when transplanting colonies I did not control for the effect of disturbance caused by manipulation on spider development, differences found in both transplanted groups are more likely to be due to changes in local conditions rather than the effect of manipulation. Manipulation could negatively affect the development of individuals and success at reproduction, for example, by affecting their foraging behavior. However, while individuals transplanted to the dry site both grew at a slower rate than the individuals in their native habitat and produced smaller clutches, I did not find any differences in the developmental variables measured between native and transplanted individuals of a dry habitat origin. If local conditions did not have an effect on the development of individuals, both transplanted groups should have shown the same response to the disturbance caused by manipulation of colonies. Thus, although it is not possible to completely rule out any effect of the manipulation on the development and foraging behavior of the transplanted individuals until the proper controls are conducted, results support the hypothesis that among environmental effects, local conditions in resource levels and temperature are in part causing the differences in development found between native and transplanted individuals of the same origin.

Transplant results suggest that dry and wet populations are differentially affected by local conditions and seem to have diverged in characters affecting their fecundity (clutch size). Although there was a tendency to larger clutch sizes in wet habitats for both native (W) and transplanted (DW) individuals than in dry sites, a significant origin effect and the absence of an interaction between origin and rearing environment indicates that individuals of a dry versus wet habitat of origin have a different performance in both dry and wet habitats. Given that the link between foraging rate-growth rate-fecundity in spiders can be determined by

differences in aggression, and that those differences in aggression levels can have a genetic basis (Arnqvist and Henriksson 1997; Hedrick and Riechert 1989) it is possible that wet and dry *P. bistriata* populations have diverged in their aggression levels as found for other spiders adapted to dry environments (Riechert and Hall 2000). In fact, dry native individuals interact more aggressively during group prey capture than native individuals at wet sites (Fernández Campón 2007), and behavioral essays performed in native and transplanted populations suggests that there is a behavioral dry and wet ecotypes (Fernández Campón 2008). Dry and wet populations differ in the level of plasticity for the tendency to forage in groups. Tendency to capture and share prey between populations can affect the amount of food taken by colony members and how that food is distributed which in turn can affect their fecundity. While individuals from wet populations do not change their tendency to forage in groups under different resource levels, individuals from dry populations show a plastic behavior. They have a greater tendency to forage in groups in dry sites when prey levels are low and decrease that tendency when under higher prey levels in wet habitat.

Differences in foraging behavior may explain the lower growth rate and smaller clutch sizes of individuals of the WD group compared to W individuals. However, these behavioral differences do not explain the higher success of DW individuals than W individuals in wet habitat. There might be other traits (e.g., physiological) that can explain the divergence in fecundity found: dry and wet populations might differ in the efficiency to allocate resources into the production of eggs (Hassall et al. 2005).

Similar results showing transplanted individuals performing better than native ones were found in other studies for traits such as intrinsic growth rate (usually correlated with fecundity) and survivorship (Berven 1982; Riechert and Hall 2000; Pardo and Johnson 2005). Although native individuals are expected to perform better in their local habitat, when transplanted individuals do better, these individuals have evolved in the more stressful environment. DW individuals seem to be taking advantage of a richer site and increase their reproductive success as compared to D individuals. This does not mean that the dry ecotype performs better under all conditions. In order to conclude that it is necessary to follow individuals for more than a generation and to examine other fitness related traits (e.g., susceptibility to pathogens, which may be more common in wet habitats). Further examination of behavioral and physiological traits in *P. bistriata* would help understand adaptations this species might have to inhabit different environments.

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