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More sharing when there is less: insights on spider sociality from an orb-weaver's perspective

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I examined the potential genetic and environmental determinants of population differences in the foraging behaviour of the colonial spider *Parawixia bistriata* by using reciprocal transplant and prey manipulation experiments. The population differences noted from a previous study are primarily associated with the degree to which this spider captures prey as a group: *P. bistriata* show a higher frequency of group capture of prey in dry habitats with lower prey levels than in wet habitats where prey levels are higher. I recorded data on the tendency to capture and feed in groups and the number of individuals feeding on that prey. The transplant experiments revealed population differences in the tendency to capture prey as a group. Individuals from dry habitat showed a greater tendency to participate in group capture and feeding of prey in their native habitat than did individuals from wet habitat or than individuals that were transplanted to dry and wet habitats. In addition, the size of capture and feeding groups showed a significant habitat effect. Individuals from wet habitat did not differ in their tendency to attack prey when transplanted to dry habitat, suggesting that *P. bistriata* from wet habitat represents an ecotype that lacks behavioural plasticity. In contrast, individuals from dry habitat showed a plastic response. Potential causes of the behavioural plasticity shown by spiders from dry habitat are discussed. Group-foraging behaviour can have a significant effect on the fitness of these spiders, as suggested by their success under low prey conditions.

Keywords: behavioural plasticity; group foraging; orb-weaving spiders; *Parawixia bistriata*; reaction norm

Social spiders constitute foraging societies in which individual foraging success is thought to drive traits of the group (Whitehouse & Lubin 2005). Spiders are usually aggressive, and solitary individuals often cannibalistic. Of all the described species of spiders, less than 1% show some level of sociality (Uetz & Hieber 1997). Thus, the examination of foraging behaviour and its response to environmental variables seems relevant to the study of the conditions under which sociality in spiders can arise.

Populations of the orb-weaving spider *Parawixia bistriata* occupying habitats with high versus low prey availability differ in elements of their foraging behaviour (Fernández Campón 2007). Individuals from wet habitats with high prey levels have a lower tendency to engage in group prey capture, while spiders from dry habitats with lower prey availability have a higher tendency to engage in collective prey capture. This finding is unusual. Higher levels of sociality under lower prey conditions is opposite to what has been reported for other social species (Avilés 1997; Uetz & Hieber 1997). In addition, despite differences in prey levels between habitats, fitness-related traits (number of eggs per sac) are similar in the two habitat types (Fernández Campón 2005). Differences in group capture and feeding of prey could result from genotypic adaptation to local environment, phenotypic plasticity or genetic differences in the level of plasticity between populations.

The extent to which plasticity in a behavioural trait is favoured in a system depends on the relationship between generation time and the temporal and spatial scales over which environmental variation is experienced (Levins 1968). If changes in the environmental conditions occur within the life span of the individual (either temporally or spatially), a genotype with a plastic reaction norm that can respond to those changes is favoured (Moran

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1992). Alternatively, plasticity will be selected against in a stable environment if there are fitness costs to maintaining a plastic genotype. There may be costs involved in acquiring information about the environment to respond in a plastic way (DeWitt et al. 1998). For example, individuals that show plasticity in foraging activity in response to the presence of predators may incur fitness costs because the time available for other activities, such as foraging, are reduced. In an environment with no predators, alert individuals will spend less time foraging than individuals that are not sensitive to the presence of predators (Bishop & Brown 1992).

It is possible to examine the sources of variation in behaviour by conducting studies at the population level. Studies on geographical variation in behaviour involve comparisons of the average phenotype expressed by individuals making up those populations. The reaction norm is compared across populations to test whether observed differences are due to phenotypic plasticity or local adaptation. The reaction norm, in this case, represents the mean phenotypic response of individuals of a population expressed under different environments. To compare reaction norms, it is necessary to subject individuals to different environmental conditions. This is usually accomplished through reciprocal transplants.

In *P. bistriata*, it is possible that behavioural plasticity underlies the observed population differences in the tendency to form foraging groups. If the behavioural differences shown by individuals are plastic, we would expect transplanted individuals to behave similarly to the natives in each habitat (same reaction norm). Plasticity in foraging behaviour underlying differences between individuals from different source plants has been shown in grasshoppers of the genus *Melanoplus* (Orthoptera: Acrididae; Thompson 1999). Nymphs hatched from eggs collected in the field from plants differing in their quality as a food source (source environment) were exposed to their source plant and to a plant of different quality. Regardless of the source environment, the grasshoppers showed diet-induced behavioural plasticity that enhanced feeding performance on hard (low-nutrient) plant diets.

Behavioural differences in foraging behaviour between populations of *P. bistriata* could also reflect ecotypic variation rather than behavioural plasticity, with dry and wet populations showing respective 'group foraging' and 'solitary foraging' ecotypes. Riechert & Hall (2000) found evidence of behavioural ecotypes in the spider *Agelenopsis aperta* (Agelenidae), although not in a social context, after performing reciprocal transplants of *A. aperta* from arid and riparian habitats. The authors describe the existence of fearful and aggressive behavioural phenotypes in each habitat type, which correspond to predation and resource levels found in those habitats. Transplanted individual showed the same behavioural phenotype as in their native habitat, which indicates the absence of plasticity in their response towards predators and prey levels.

Individuals from dry and wet habitats may also show different levels of plasticity in behaviour resulting from selection on the norm of reaction. Habitat differences in temporal patterns of environmental variables can lead to different norms of reaction (Moran 1992). If one of the habitat types is more variable in factors relevant to foraging behaviour (e.g. prey availability), a plastic reaction norm would be expected in such a habitat, while a non-plastic one would be favoured in the more stable habitat type. This is the case in soapberry bugs, although in the context of male mating tactics, not foraging. Spatial and temporal variability in sex ratio of the rearing environment also affect levels of behavioural plasticity (Carroll & Corneli 1999). Individuals from environments with more variable sex ratio are more plastic behaviourally, with the expression of mate-guarding behaviour changing as a function of sex ratio. Individuals from populations with a stable sex ratio, however, do not vary the extent to which they guard their mates even when expected under conditions of a female-biased sex ratio.

To discern which of the three alternatives mentioned above might underlie the observed difference in grouping tendency during foraging in populations of *P. bistriata* between wet and dry habitats, I used feeding manipulations and reciprocal transplants. These analyses further provide some assessment of the extent to which observed population differences in foraging patterns are adaptive.

METHODS

Study Species

Parawixia bistriata (Araneidae) is a territorial group living orb-weaver. Although it inhabits diverse habitats, it is typically found in semiarid habitats in southern South America (Levi 1992).

The development of this univoltine spider is completed after the seventh moult (Sandoval 1987) and its phenology can vary depending on the habitat type (Fernández Campón 2005). In the wet sites of this study, adults are found in the austral summer, at the end of December and January, while in the dry sites, adults are found in early autumn, between March and April.

Colonies are usually composed of siblings, although some unrelated individuals can be found when colony joining occurs. Individuals live in colonies during their immature stages. Colonies are started when adults disperse after moulting, and subsequently mate and lay eggsacs. Dispersal in this social species may be an adaptation to semiarid environments by frequently relocating the colony to suitable microclimates within these environments (Fowler & Diehl 1978; Fowler & Gobbi 1988).

Individuals within a colony share a diurnal retreat. They emerge from the retreat at dusk and build their individual capture webs. Webs are attached side by side, sharing common framelines and forming vertical sheets. Individuals defend their capture webs from conspecifics, but when group foraging of prey occurs, neighbour spiders enter the web of the resident spider, where the prey was caught. Previous studies have reported that group-foraging expression is facultative depending on the size of the prey (Fowler & Diehl 1978; Fowler & Gobbi 1988; de Carvalho 1998).

Analysis of behavioural sequences during solitary and group foraging events suggests that the occurrence of

group foraging results from the impossibility of defending the capture web and the prey from other spiders that try to participate in foraging (Fernández Campón 2007). There are potential risks of injury to an individual that joins in a prey capture event because individuals engage in agonistic interactions during the course of group foraging. Injuries inflicted by large prey are also a potential risk. These are potential fitness costs associated with attempted capture of large prey items.

Study Site

All study areas were situated in the Chaco region of northeastern Argentina (26°S) 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 levels and temporal variability in precipitation patterns differ between respective dry and wet study sites.

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 Formosa province of Argentina, Wet 1 at a provincial reserve, Guaycolec (26°10′S, 58°12′W), and Wet 2 at a private reserve, El Bagual (26°10′S, 58°56′W). The dry sites were located close to the town of Pampa del Infierno (26°30′S, 61°10′W) in Chaco province, Dry 1 on the Allende family ranch 7 km northeast of Pampa del Infierno and Dry 2 on a railroad right of way on the eastern side of town on public-owned land. (I found that, owing to human disturbance, it was not possible to complete experimental manipulations at the site Dry 2. Thus, this site only provided data on the foraging behaviour of spiders at native colonies).

Both habitat types have a marked dry season in the winter and wet summers during which 80–90% 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 (Fernández Campón 2005).

Insect availability

I collected the insect availability data over three sampling periods for each site during the field season extending from October 2002 to January 2003. Each sampling period lasted between 2 and 8 days. Insect availability in the two wet sites (measured as the average insect dry biomass sampled by a Malaise trap per night) was almost twice the biomass sampled in the site Dry 1 (mean ± SE: Dry = 0.159 ± 0.018 g; Wet = 0.277 ± 0.037 g). Occurrence of group foraging has been reported to occur when the size of the prey is larger than the size of a spider (Fowler & Diehl 1978; Fowler & Gobbi 1988). Thus, it is important to this study to learn whether wet and dry habitats differ with respect to the frequency and variability of insects of different size (i.e. is there a greater representation of large insects in dry or wet habitat? Is the frequency of insects in one of the habitat types more variable? I first examined the insect data assigning insects into two size classes: (1) insects smaller than a spider and (2) insects of the same size or larger than a spider. To control for ontogenetic effects in behavioural differences I only worked with sixth-instar individuals. Body length of a sixth-instar spider is 9.87 ± 0.1 mm; thus, I used 10 mm as a cutoff between the insect size classes. To test for differences in the frequency of insects between sites and between size classes, I first performed a general linear model (GLM). I then examined only the data from insects in the large size class, assigning them to three size classes corresponding to spiders' body length (bl): 1–1.5 bl, 1.5–2 bl and longer than 2 bl (10–14.9 mm, 15–19.9 mm and 20 mm or longer). I performed a GLM and estimated the coefficient of variation to test for differences in frequency and variability among sites. The analysis of large prey frequency allowed me to examine in more detail changes within large insect prey that may affect expression of group foraging.

Trap insect data have been shown to be a biased representation of prey that spiders consume (Eberhard 1990). In this study, the bias was similar at all sites because the same traps were used at each site. Thus, the trap data are useful for site comparisons. However, although traps were set during the activity period of *P. bistriata* individuals, the insects collected were a rough estimate of those captured by the spiders.

Experimental Methods

Reciprocal transplant

I conducted a transplant experiment to determine whether the behavioural differences shown by *P. bistriata* populations were the result of genetic divergence or phenotypic plasticity in response to variation in prey availability.

The transplants were conducted in two stages; the second stage was completed to augment sample sizes, given the low colony establishment success achieved in the first transplant session. In the first stage of the experiment, one colony of wet origin was established in November 2001 after transplantation to the site Dry 1 in June, and two colonies of a dry origin were transplanted to the site Wet 2. I transplanted these colonies early in December 2001 and recorded data a month later. In the second stage, colonies transplanted to Dry 1 were collected in Formosa city (25 km south and 70 km northeast from Wet 1 and Wet 2, respectively) when they were third- or fourth-instar nymphs. Data collection started after individuals had overwintered in the dry site for a period of 4 months. The transplantation of dry colonies to wet sites was carried out when individuals from colonies at a site located in the vicinity of Dry 1 were at the third or fourth instar. Data collection started 2 months after transplantation. Overall, I recorded data on 24 native colonies in dry sites (first year: 10; second year: 14); 18 native colonies in wet sites (first year: nine; second year: nine); 11 colonies of dry site origin transplanted to wet sites (first year: two; second year: nine); and six colonies of wet origin transplanted to one of the dry sites (first year: one; second year: five).

No transplants were made within the immediate vicinity of existing colonies (minimum distance to each native

colony was 200 m). The transplanted colonies were placed in each locality 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. The protocol for colony transplantation is described in Fernández Campón (2005). When transplanting colonies, I did not control for the effects of the disturbance caused by manipulation during colony transplantation or of the suitability of the specific sites to which I transplanted the colonies for *P. bistriata* individuals. Transplanting colonies within their native habitat would have served as a control for these two effects. I chose to use a conditioning period (1–2 months) instead. Thus, I would expect the two effects to be minimal. During this period, colonies could move to better microhabitats: colony relocation occurs in native populations of *P. bistriata* (Sandoval 1987; F. Fernández Campón, personal observation) as well as in other social species when microhabitat conditions are not suitable (Smith 1985). In fact, most of the colonies in this study moved from the specific microsite to which I transplanted them.

Prey manipulation experiment

I conducted a manipulative experiment between October 2001 and January 2002, and between October 2002 and January 2003 to quantify the effect of prey size on the tendency to forage in groups. Data on native individuals have been previously analysed (Fernández Campón 2007). Here, I include data on individuals from transplanted colonies to further examine the existence of genetic versus environmental sources of variation in foraging behaviour of *P. bistriata* towards prey of different size.

The experiment consisted of feeding trials in which a prey item was offered to a focal spider positioned on its capture web. Observations were made using the focal-animal (or group) method (Lehner 1996). I used moths as prey: this reduced the variability in prey profitability that would have been encountered if a variety of insect prey were used. Moths are also familiar prey to *P. bistriata* and were readily obtained through the use of a light trap. Prior to its release on a web, I weighed each moth with an Acculab field balance (model no. PP-2060D, Sartorius Group, Goettingen, Germany).

The live moths were offered to spiders within one or two nights of capture. The spider used as the focal individual was one that was positioned on the hub of its capture web facing the ground, the standard foraging position shown by *P. bistriata*. Other constraints on selection of a focal individual were: (1) the focal spider could not be feeding on a prey item at the time the moth was released, (2) the focal individual was at the sixth instar in age, and (3) at least four of its nearest neighbours were positioned in foraging mode at the hubs of their webs. These criteria reflect the following assumptions: (1) spiders that are not feeding are more likely to be responsive to the offered prey item, (2) by having spiders in the adjacent webs, there would be neighbours 'available' to participate in the capture and feeding of the prey item offered, (3) because the response of individuals towards conspecifics and prey of different size can change with the developmental stage (de Carvalho 1998), I chose only sixth-instar focal individuals to control for ontogenetic effects in foraging behaviour.

I estimated the tendency of individuals to attack prey of different sizes by recording the number of trials in which a prey item was captured and consumed by a group or a solitary individual. I also estimated the size of capture and feeding groups by recording the number of spiders participating in the capture of a given prey item and the number feeding on that prey. The number of spiders participating in a capture is defined as the total number of individuals that attacked the moth from first attack to its being subdued (cessation of struggling). The number of spiders feeding on a given moth was defined as the maximum number of spiders observed feeding on the prey during a 1-min interval in the feeding sequence, which ended with complete consumption or with the partitioning of the prey into pieces.

Tendency to forage in a group

To identify the sources of variation (genetic or environmental) in the tendency to attack prey as a groups, I analysed a data set that included frequencies of solitary- and group-foraging trials of individuals from both native and transplanted colonies during the 2 years of this study. I used the variables 'habitat of origin' and 'rearing environment' to examine whether the observed behavioural differences between native populations were due to environmental (plasticity) or ecotypic variation. The behavioural response measured was the tendency to attack and feed on prey as a function of prey size; thus, the model also included the size of the prey as a continuous variable. Finding a significant effect of habitat of origin would indicate that genetic divergence between populations was responsible for the difference in the tendency to forage in a group as a function of prey size. Alternatively, a significant effect of rearing environment would indicate that spiders show a flexible response to forage in a group depending on changes in local conditions. A significant interaction between habitat of origin and rearing environment would indicate that individuals from the different populations have diverged in the reaction norms with different degrees of plasticity shown in their behaviour. Finally, finding that both main effects were significant but not the interactions would indicate that dry and wet populations show similar levels of plasticity in the tendency to forage in group but they differ in their mean reaction norm, with one population showing a higher tendency to forage in a group over all prey sizes offered. This would also be indicative of genetic divergence in reaction norms.

I analysed these data with a logistic regression using the GENMOD procedure in SAS (SAS Institue, Cary, NC, U.S.A.). Variables included in the model were group capture (1: group capture; 0: solitary capture) as the dichotomous response and prey mass (g, wet weight), year (2001–2002 and 2002–2003), habitat of origin and rearing environment as the explanatory variables. I repeated this same analysis for data on feeding events, but in this case, the response variable was the occurrence of group feeding.

Size of the capture and feeding groups

For the trials in which the prey item was captured or fed on by a group of individuals, I examined whether the size of the prey item influenced the size of the capture or feeding group, and as before, whether there were genetic or environmental effects on that response. Data on the size of the capture and feeding groups consisted of small integer counts, which violated the assumptions of parametric statistical tests. I applied a general 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 (deviance and df) indicated that the data were overdispersed. 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. I selected the model that presented the best fit to the data using a likelihood-based chi-square test (Stokes et al. 2000). In these analyses, group size (the number of spiders participating in the capture of or feeding on a prey item) was the response variable. As with the logistic regression models described above, prey mass, year, habitat of origin and rearing environment were the explanatory variables.

In both logistic and Poisson regressions, the program calculated estimates of the parameter vector β corresponding to each of the explanatory variables. The sign of β tells the direction of the effect of the explanatory variable (whether it is positive or negative) on the response variable. Using β it is possible to calculate the odds ratio (in the logistic regression) and the predictor estimates (in the Poisson regression), which indicates the magnitude of the effect on the response variable.

RESULTS

Insect Availability

Insect prey smaller than spiders were more frequent than large prey in both dry and wet habitat types (mean ± SE: small prey: 109.26 ± 13.53; large prey: 8.42 ± 1.03; GLM, prey size effect: $F_{1,18} = 56.25$, $P = 0.00$). When contrasting wet and dry sites, there were no differences in the mean frequency of small (mean ± SE: Wet 1: 89.71 ± 6.36; Wet 2: 136.49 ± 32.47; Dry: 101.59 ± 22.93) and large (mean ± SE: Wet 1: 11.13 ± 2.35; Wet 2: 8.44 ± 0.84; Dry: 5.70 ± 0.69; GLM, site effect: $F_{2,18} = 1.05$, $P = 0.37$; site × prey size: $F_{2,18} = 1.16$, $P = 0.33$) insect prey.

Although differences between sites in the frequency of large insects were not significant (see above), when analysing large insect data in detail, I found differences in the frequency of insect corresponding to 1.5–2 bl (15.0–19.9 mm; GLM; site × prey size: $F_{1,27} = 6.47$; $P = 0.00$). The dry sites had a significantly lower frequency of insects within this size class than the two wet sites (pairwise comparisons after Bonferroni adjustment: Wet 1 versus Wet 2: $P = 1.00$; Dry versus Wet 1: $P = 0.00$; Dry versus Wet 2: $P = 0.04$; Fig. 1a). Variability in the frequency of large insects increased with the size of the insects. As with the frequency, there were differences between sites in the second size class. In this case, variability was higher in the dry site than in the two wet sites (Fig. 1b).

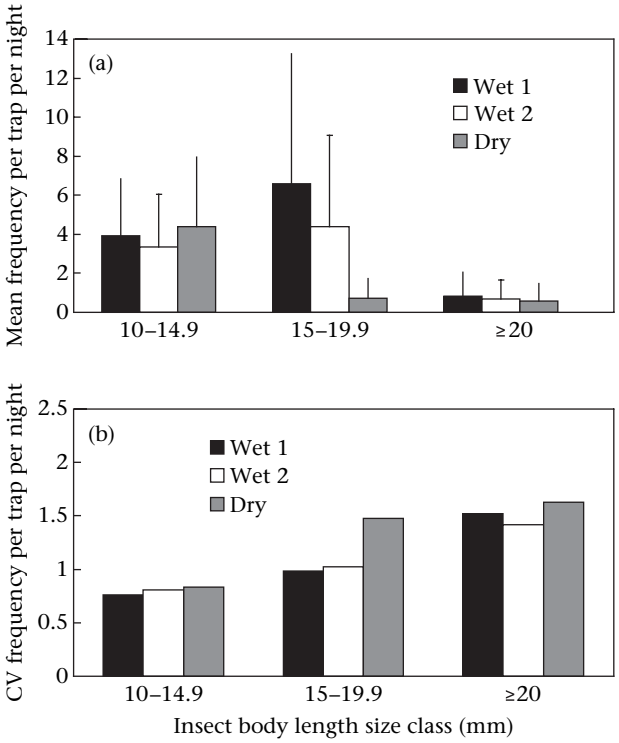

Figure 1. Frequency and variability of insects with a body length longer than a sixth-instar spider (mean ± SE: 9.87 ± 0.1 mm, $N = 113$) in dry and wet sites. (a) Average frequency of insects sampled per Malaise trap per night (bars indicate SD); (b) coefficient of variation of the average frequency of insects sampled per trap per night corresponding to the data shown in (a).

Tendency to Attack and Feed on Prey as a Group

Individuals from the dry habitat showed a higher tendency to capture prey as a group than those transplanted to either dry or wet sites and than those from wet habitat (Fig. 2) This result was seen in the significant interaction between rearing environment and habitat of origin (chi-square test: $\chi^2_1 = 8.64$, $P < 0.01$; Table 1) and when performing contrasts between the four treatment groups. The contrasts between groups indicated that the tendency to attack prey as a group was significantly higher for individuals from dry habitats than for the other three groups ($\chi^2_1 = 4.82$, $P = 0.03$; Table 2). In addition, the results of the logistic regression for the proportion of group captures among native and transplanted colonies showed a significant overall effect of prey size ($\chi^2_1 = 44.22$, $P < 0.01$).

The tendency to feed as a group did not show an effect of habitat of origin ($\chi^2_1 = 0.06$, $P = 0.81$), rearing environment ($\chi^2_1 = 1.84$, $P = 0.17$) or year ($\chi^2_1 = 3.35$, $P = 0.07$). The size of the prey was the only significant variable ($\chi^2_1 = 81.65$, $P < 0.01$; Fig. 3). However, when the two habitats of origin were tested independently, differences between native and transplanted individuals were found.

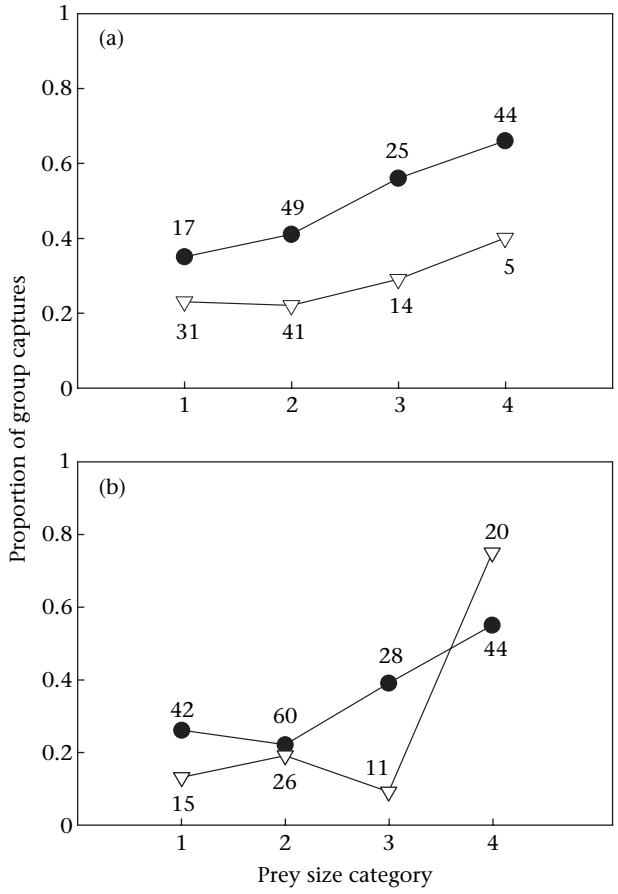

Figure 2. Comparison of the proportion of group capture events in native (●) and transplanted (▽) colonies from dry (a) and wet (b) habitats. Numbers over bars indicate the total number of trials per size class. Data on prey size were pooled into four prey size categories for graphic representation. Prey size categories were defined as a percentage of the average mass of a sixth-instar spider (mean ± SE: 0.196 ± 0.005 g, $N = 215$) as follows: category 1, 0–25%; category 2, 25.1–50%; category 3, 50.1–75%; category 4, >75%.

Individuals from dry habitat situated in their native habitat showed a higher tendency to feed in groups than individuals from dry origin transplanted to wet sites (prey size: $\chi^2_1 = 27.30$, $P < 0.01$; rearing environment: $\chi^2_1 = 5.41$, $P = 0.02$). Individuals from wet habitat, however, showed similar tendencies to feed in groups whether they were in their native habitat or transplanted (prey size: $\chi^2_1 = 51.02$, $P = 0.01$; rearing environment: $\chi^2_1 = 0.00$, $P = 0.96$).

Table 1. General linear model analysis (PROC GENMOD; binomial distribution of errors and logit link) of frequency of trials in which group and solitary captures occurred for native and transplanted groups

Source	df	χ^2	P
Prey mass	1	44.22	<0.01
Rearing environment	1	1.43	0.23
Habitat of origin	1	1.45	0.23
Year	1	0.30	0.59
Rearing environment×habitat of origin	1	8.64	<0.01

Deviance = 559.90 with 477 df.

Table 2. Contrasts of the interaction between rearing environment and habitat of origin in the general linear model of the tendency to capture prey in groups for native and transplanted spiders (see Table 1)

Contrasts	β	Odds ratio ($CI_{Wald\ 95\%}$)	χ^2	P
DD vs WW	0.54	1.71 (1.05–2.77)	4.82	0.03
DW vs WW	−0.38	0.68 (0.38–1.23)	1.61	0.21
WD vs WW	−0.37	0.69 (0.37–1.28)	1.39	0.24

DD: dry in dry, natives from dry habitat; WW: wet in wet, natives from wet habitat; DW: dry in wet, individuals from dry habitat transplanted to wet habitat; WD: wet in dry, individuals from wet habitat transplanted to dry habitat. The group WW was used as the reference group.

The size of the prey offered during experiments showed no significant relationship with trial date (Spearman rank correlation: $r_S = 0.06$, $N = 544$, $P = 0.19$). The time at which each trial took place, however, showed a weak but significant negative correlation with prey size offered ($r_S = -0.11$, $N = 540$, $P = 0.01$). A logistic regression conducted to test the effect of trial timing on the likelihood of group capture showed no significant effect (type III test: $\chi^2_1 = 0.01$, $P = 0.93$). Thus, although larger prey

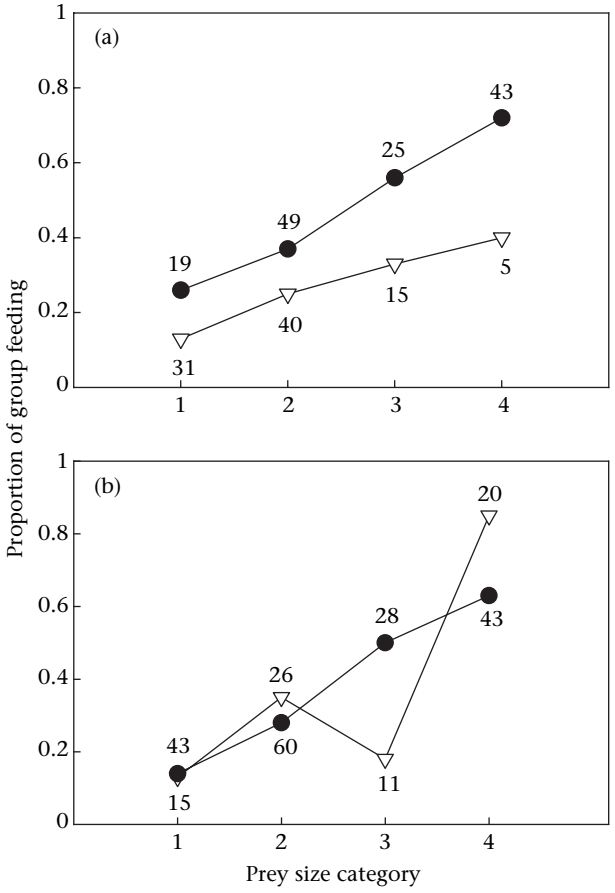

Figure 3. Comparison of the proportion of group feeding events in native (●) and transplanted (▽) colonies from dry (a) and wet (b) habitats. Numbers over bars indicate the total number of trials per size class. Data on prey size were pooled into four prey size categories for graphic representation, as in Fig. 2.

Table 3. General linear model analysis (PROC GENMOD; Poisson distribution of errors and log link) of the size of capture group (number of spiders participating in group capture) in native and transplanted individuals from dry and wet habitats

Source	ndf	ddf	*F*	*P*
Prey mass	1	166	13.50	<0.01
Rearing environment	1	166	0.37	0.55
Habitat of origin	1	166	0.17	0.68
Year	1	166	2.88	0.09
Prey mass×rearing environment×habitat of origin	3	166	2.61	0.04

Deviance = 67.41, with 166 df. Variance adjusted for underdispersion using deviance. Groups used as reference were: wet habitat, wet origin, second season, wet native.

tended to be offered earlier in the evening (significant negative correlation between prey size and time), the time when the prey item was offered did not influence the occurrence of group foraging.

Group Size During Capture and Feeding

The number of spiders in a capture group increased with the size of the prey in all four treatments (Table 3). In addition, individuals from wet sites that had been transplanted to dry sites showed a more rapid increase in group size as a function of prey size than other treatment groups (Fig. 4). This pattern was seen in the interaction effect between prey size, rearing environment and habitat of origin. The results of the contrasts that indicated that individuals from wet sites that had been transplanted to dry sites showed a significantly stronger response to increases in prey size than did other classes of individuals (Table 4). Responses to increases in prey size also tended to be stronger for spiders tested in their native dry habitat than for those tested in their native wet habitat (see Table 4; $P = 0.06$).

The size of the feeding group showed a similar pattern as that of the capture group. The number of individuals in the feeding group increased with the size of the prey items ($\chi^2_1 = 20.19$, $P < 0.01$), although feeding-group sizes of both native and transplanted individuals in wet habitat significantly increased with prey size (significant prey mass × habitat of origin × rearing environment effect; Fig. 5, Table 5). There was also a significant effect of year ($\chi^2_1 = 34.84$, $P < 0.01$) on the incidence of group feeding. Predictor estimates indicated that group feeding was 50% more prevalent during the first year than during the second ($\beta = 0.40$, predictor estimate = 1.50, $\chi^2_1 = 35.87$, $P < 0.01$). However, the magnitude of the effect of the rearing environment was stronger than the year effect ($\beta = 1.97$, predictor estimate = 7.15, $\chi^2_1 = 11.04$, $P < 0.01$). In addition, multiple contrasts between data at each rearing environment during each year showed that group sizes within each environment type did not differ between years (Table 6).

DISCUSSION

I examined mechanisms underlying observed differences in foraging behaviour between spiders from habitats with

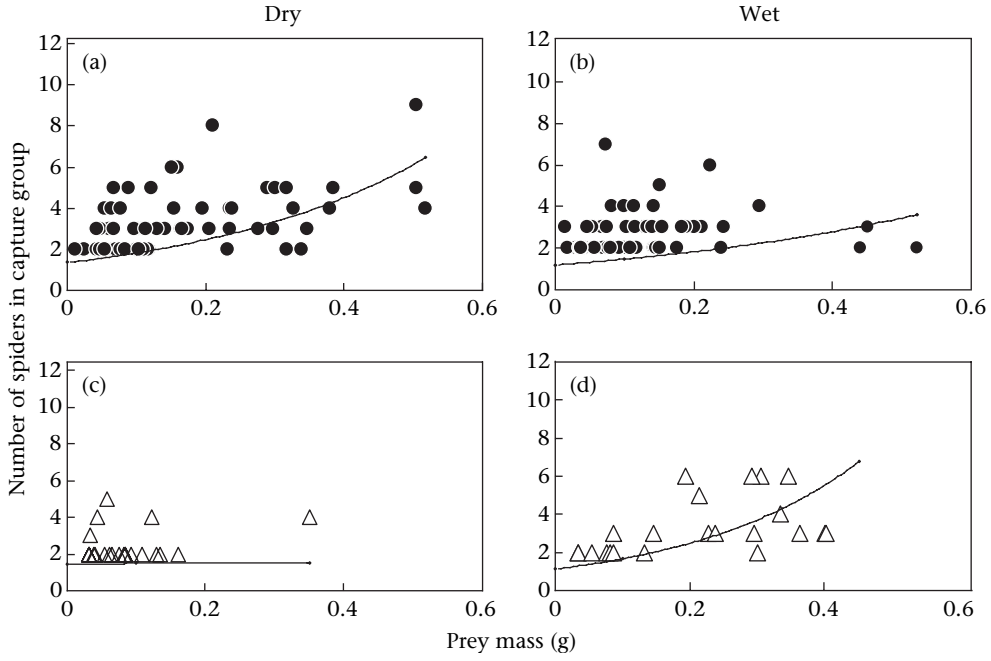

Figure 4. Number of spiders participating in group prey capture as a function of prey size in native (●) and transplanted (△) colonies from dry and wet habitats. (a) Native individuals from dry habitat, (b) native individuals from wet habitat, (c) individuals from dry habitat transplanted to a wet site, (d) individuals from wet habitat transplanted to the dry site. Equations plotted in the graphs are based on the estimates of parameters obtained for the Poisson regression described in Table 2. For each of the groups, the equations were as follows: Dry Native, $Y = e^{(0.3149 + 2.5886X)}$; Wet Native, $Y = e^{(0.1783 + 2.1218X)}$; Transplant to Wet, $Y = e^{(0.3822 + 0.0798X)}$; Transplant to Dry, $Y = e^{(0.1110 + 3.9891X)}$.

Table 4. Contrasts of the interaction between prey mass, rearing environment and habitat of origin in the general linear models of the size of the capture and feeding groups for native and transplanted spiders (see Tables 3, 4)

	Contrasts	β	Predictor ($CI_{Wald\ 95\%}$)	χ^2	*P*
Capture groups	DD vs WW	0.99	2.68 (0.96–7.50)	3.54	0.06
	DW vs WW	−0.23	0.79 (0.09–6.72)	0.05	0.83
	WD vs WW	1.52	4.58 (1.56–13.50)	7.63	<0.01
Feeding groups	DD vs WW	1.59	4.93 (1.28–18.95)	5.41	0.02
	DW vs WW	0.55	1.73 (0.14–21.68)	0.18	0.67
	WD vs WW	2.75	15.68 (4.05–60.72)	15.87	<0.01

DD: dry in dry, natives from dry habitat; WW: wet in wet, natives from wet habitat; DW: dry in wet, individuals from dry habitat transplanted to wet habitat; WD: wet in dry, individuals from wet habitat transplanted to dry habitat. The group WW was used as the reference group.

different prey levels (dry versus wet habitats). I tested three hypotheses: (1) the existence of phenotypic plasticity in the behavioural traits examined; (2) the presence of ecotypes with divergence of behavioural traits in individuals from different habitats of origin; (3) divergence in the reaction norm between individuals from different origins, with individuals from dry and wet habitats differing in their levels of behavioural plasticity. The results from the transplant experiment suggest that individuals from dry and wet habitats showed different levels of plasticity in their tendency to forage in groups, supporting the hypothesis of divergence in the reaction norms. In addition, the larger number of individuals participating in capture and feeding groups in dry habitats seems to be a response to environmental factors with no effect of habitat of origin.

Divergence in the Tendency to Forage in Groups and Some Thoughts on Its Causes

There were population differences in the degree to which individuals engaged in group capture. While both dry and wet populations of *P. bistriata* showed some group foraging, populations of wet habitat origin showed no significant context variability in their tendency to participate in group capture of prey, lacking plasticity for the trait. However, individuals from the dry habitat populations showed plasticity in this trait: in their native habitat, which afforded lower levels of prey, individuals showed a higher tendency to forage in groups than did individuals that were transplanted from dry to wet habitats.

A higher tendency to forage in groups in habitats with low prey abundance is contrary to what is typically found

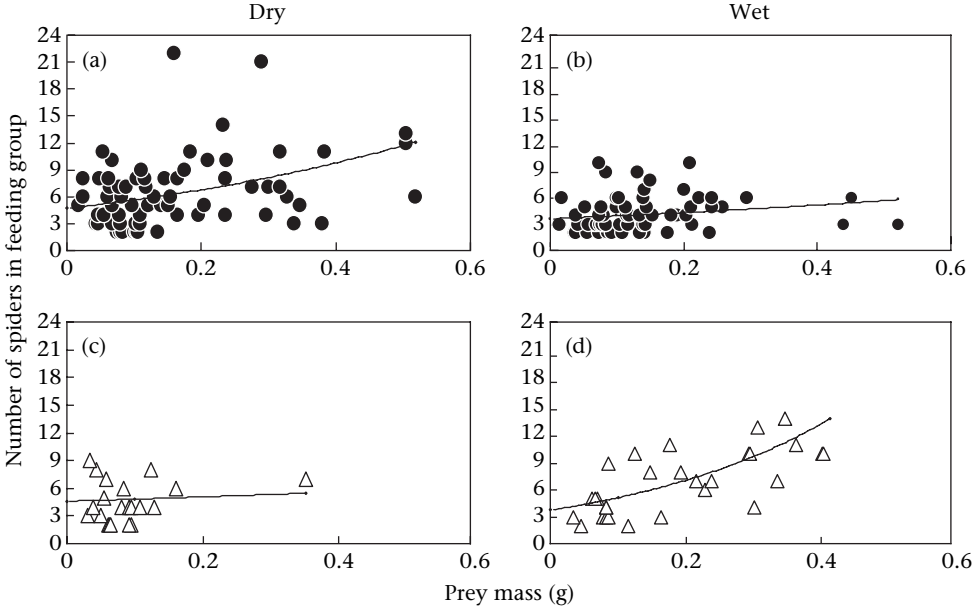

Figure 5. Number of spiders participating in group-feeding trials as a function of prey size in native (●) and transplanted (△) colonies from dry and wet habitats. (a) Native individuals from dry habitat, (b) native individuals from wet habitat, (c) individuals from dry habitat transplanted to a wet site, (d) individuals from wet habitat transplanted to the dry site. Equations plotted in the graphs are based on the estimates of parameters obtained for the Poisson regression described in Table 3. For each of the groups, the equations were as follows: Dry Native, $Y = e^{(1.5495 + 1.8244X)}$; Wet Native, $Y = e^{(1.2936 + 0.9045X)}$; Transplant to Wet, $Y = e^{(1.5251 + 0.2315X)}$; Transplant to Dry, $Y = e^{(1.3180 + 3.1937X)}$.

Table 5. General linear model analysis (PROC GENMOD; Poisson distribution of errors and log link) of the size of feeding groups (number of spiders feeding in a group) in native and transplanted individuals from dry and wet habitats

Source	ndf	ddf	*F*	*P*
Prey size	1	175	17.64	<0.01
Rearing environment	1	175	0.33	0.57
Habitat of origin	1	175	1.98	0.16
Year	1	175	30.44	<0.01
Prey mass×rearing environment×habitat of origin	3	175	18.42	<0.01

Deviance = 200.34 with 175 df. Variance adjusted for underdispersion using deviance.

in social spiders (Riechert 1985; Avilés 1997; Uetz & Hieber 1997). Most social species of spiders are found in wet tropical and subtropical areas (Avilés 1997). The lower competition for resources in prey-rich habitats is thought to promote higher tolerance among conspecifics and a social lifestyle (Riechert 1985). In addition, even some solitary species are reported to aggregate in sites with locally abundant prey levels (Rypstra 1986). Thus, *P. bistriata*'s greater tendency to forage in habitats offering lower resource is unusual.

It is possible that foraging-related forces other than prey availability have driven group living in *P. bistriata*. For example, joining webs into larger capture sheets may allow individuals to exploit niches unavailable to solitary individuals (e.g. open areas; Whitehouse & Lubin 2005), particularly in sites where prey are scarce. In addition, genetic forces such as inclusive fitness benefits might have facilitated group living in *P. bistriata* by extending the period of aggregation of siblings. One possible evolutionary pathway for sociality in spiders is the subsocial route. This route originates with prolonged association of siblings from the eggsac and may be influenced by kin selection (Shear 1970). Thus, the fact that colonies are made up of siblings suggests that there may be inclusive fitness benefits in sharing food with other colony members.

Table 6. Contrasts of the interaction between prey mass, rearing environment and year in the general linear model of the size of the feeding groups for native and transplanted spiders

Contrasts	β	Predictor ($CI_{Wald\ 95\%}$)	χ^2	*P*
Dry-1st vs Wet-2nd	1.84	6.29 (1.22–32.40)	4.83	0.03
Dry-2nd vs Wet-2nd	1.45	4.28 (1.30–14.05)	5.75	0.02
Wet-1st vs Wet-2nd	−1.59	0.20 (0.04–1.22)	3.02	0.08
Wet-1st vs Dry-2nd	−3.05	0.05 (0.01–0.31)	10.03	<0.01
Dry-1st vs Dry-2nd	0.38	1.47 (0.48–4.47)	0.43	0.50

I present contrasts using the groups Wet-2nd and Dry-2nd as reference groups. The model included the following variables: prey mass, habitat of origin, rearing environment, year, and the interaction prey mass × rearing environment × year. Dry-1st: native and transplanted individuals found in dry habitat during the first year; Dry-2nd: native and transplanted individuals found in dry habitat during the second year; Wet-1st: native and transplanted individuals found in wet habitat during the first year; Wet-2nd: native and transplanted individuals found in wet habitat during the second year.

Once group living arose, the foraging function of the colony affected behavioural traits (tendency to forage in a group) depending on local conditions of prey. For example, a reduction in the tendency to attack and feed on prey as a group could be advantageous at wet sites. When the encounter rate with prey is high, individuals probably obtain optimal feeding levels through solitary foraging, and by doing so, avoid the costs involved in group foraging, such as injury from large prey and agonistic interactions between group members.

The costs of foraging in groups would explain why individuals from wet habitat and individuals transplanted to wet habitat showed a lower tendency to forage in groups than individuals in dry habitat. However, it does not explain the absence of behavioural plasticity in individuals from wet habitat. Differences in levels of plasticity could result from selective pressures if there are costs to plasticity itself (DeWitt et al. 1998; Pigliucci 2001). At this point, *P. bistriata*'s plasticity in the tendency to capture large prey in a group does not seem to have any costs to fitness. Individuals from dry habitat transplanted to wet habitats (plastic genotype) show levels of fitness (number of eggs produced per sac; Fernández Campón 2005) that are similar to those of native individuals (fixed genotype). However, these results do not constitute definitive evidence for the lack of costs to plasticity. This is because transplants were performed when individuals were in their third and forth instars and the transplantation experiment ended after the individuals had laid eggsacs. So, it is possible that there are costs to plasticity that could be experienced at an earlier developmental stage, or that there are maternal effects expressed in the offspring of the transplanted individuals (if less yolk content in the eggs negatively affects offspring survival; Morse & Stephens 1996).

Negative selection on plastic genotypes in wet habitats could also result from correlations between traits and the tendency to forage in groups. Selection on a trait causes changes in the expression of a correlated trait, thus limiting the level of plasticity of the second trait (Merila et al. 2004). In *P. bistriata*, it is possible that selection for lower aggression levels or higher tolerance towards conspecifics leads to lower responsiveness towards prey in wet habitat. Some species show correlated behaviours across situations or behavioural syndromes (Sih et al. 2004). These can be expressed as higher aggressiveness towards prey as well as towards conspecifics (e.g. the desert spider *A. aperta*; Riechert & Hedrick 1993). Selection for higher tolerance and lower aggression could affect the tendency to forage in a group if higher levels of tolerance allow neighbours to enter a resident's web and feed on prey that lands on the resident's web without incurring costs of escalated aggression.

Habitat Differences in the Size of Groups

There were quantitative differences in capture and feeding group sizes in both wet and dry populations in response to changes in local environment. Regardless of their habitat of origin, individuals modified their

responses according to local conditions (i.e. proximally to hunger levels and ultimately to prey levels). Thus, larger capture and feeding groups were found in dry habitats that offered lower prey levels. In particular, feeding groups were larger than capture groups, indicating the presence of scroungers (individuals that feed on a prey that they have not helped to capture). The existence of scroungers has been predicted in models aiming to explain conditions under which group foraging occurs (Whitehouse & Lubin 2005). As prey size increases, it is more difficult to defend and monopolize; thus, opportunities for cheating or scrounging arise.

Differences in costs associated with joining a group under different prey levels may explain the observed differences in the size of capture groups. When an individual joins a group capture, it gains access to prey that has landed on a neighbour's web, but it also risks usurpation of its own web and of the prey landing on it. On the other hand, there are also costs associated with group capture in the form of agonistic interactions among foragers and the possibility of being injured by large prey. When prey levels are low, the chances of capturing prey on one's web are low compared to habitats with higher prey levels. This reduction in the costs to participate in a group capture together with higher hunger levels due to the lower prey availability may explain the larger capture groups found in the dry habitat compared to wet habitat.

Social spiders are considered foraging societies (Whitehouse & Lubin 2005). Models that include variables such as average size of prey caught and costs of monopolizing and sharing prey may be adequate to explain conditions under which group foraging in *P. bistriata* would occur and the foraging tactic that individuals would follow. In fact, these models are good predictors of the conditions under which cooperative hunting would evolve for carnivores such as lions and hyaenas and nonterritorial social spiders (e.g. *Stegodyphus*; Packer & Ruttan 1988). Although the size distribution of prey could promote group foraging, it is not sufficient to explain the differences in foraging behaviour in the populations of *P. bistriata* that I studied. The habitats in which populations showed a higher tendency to forage in groups did not have proportionately more large prey. The possibility of using open areas by joining webs and being able to exploit large prey by foraging in groups could explain why group foraging evolved in the species. Other variables such as costs to monopolize a prey item, costs of playing the scrounger tactic (e.g. probability of being excluded from a feeding group on a prey the spider did not caught) and hunger levels should be included in predictive models to explain between population differences in foraging behaviour of *P. bistriata*. The existence of correlated traits should also be assessed, for example, by evaluating aggression levels in a nonforaging context.

In dry habitats, where prey levels are lower and can limit reproduction, *P. bistriata*'s higher tendency to forage as a group appears to correspond with success at reproduction (Fernández Campón 2005). Therefore, it is possible that successful reproduction under low prey level conditions could depend on the extra energy obtained from prey captured as a group and the higher levels of group foraging favoured in these environments.

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