



Group foraging in the colonial spider *Parawixia bistriata* (Araneidae): effect of resource levels and prey size

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In animal groups whose focus is on juvenile growth, prey attributes and the way in which individuals have access to those prey influence the level of sociality. Models examining the evolution of group foraging predict that, if an individual is able to monopolize a prey item, it should not permit collaboration in the capture of or feeding on that prey. If monopoly is not possible, individuals should allow others to join because of the high cost of prey defensibility. Hunger stress can affect the above predictions through its effect on the perceived value of a prey item. An increase in the individual tendency to attack prey could result in more group captures at higher hunger levels when the resident spider fails to monopolize a prey item. I conducted a study on the foraging behaviour of the colonial spider *Parawixia bistriata* in habitats with different insect availability. I offered prey items of known size to spiders at their web sites and determined frequency of group capture and feeding relative to prey size. I also recorded the number of individuals participating in capture and feeding groups and interactions between the resident and other foraging spiders. Individuals showed a higher tendency to capture prey and feed in a group as the size of the prey increased. In addition, spiders from habitats with lower levels of prey (dry sites) had a higher tendency to attack prey collectively than did spiders from wet sites where prey levels were higher. Although there were no between-habitat differences in tendency to feed in groups, group sizes of foraging spiders were larger at dry sites. Levels of aggression between the resident and other foraging spiders were low over all trials, but behavioural acts involving direct interactions were more frequent in groups from dry sites.

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In social species, interactions among members of the group can have a preferential impact on different life stages of individuals, such as reproduction or juvenile growth. Thus, it is possible to classify animal groups into breeding societies and foraging societies (Whitehouse & Lubin 2005). In breeding societies, most social activities are associated with securing reproduction and the rearing and protection of offspring (e.g. social Hymenoptera: Keller & Reeve 1994; cooperatively breeding birds and mammals: Jennions & Macdonald 1994). Foraging societies, in contrast, are primarily influenced by foraging constraints, and most social activities within these groups affect individual growth (e.g. foraging, thermoregulation: Costa & Pierce 1997). Factors related to food acquisition,

such as the risks involved in obtaining access to food, the methods used to catch and distribute prey among group members, and the procedures involved in handling or consuming the food could affect the level of cooperation or social interactions within the group (Whitehouse & Lubin 2005).

Colonial spiders are a group of social species of spiders that constitute foraging societies (Whitehouse & Lubin 2005). Colonial spiders produce many young and lack maternal care, and characteristics of the group are dominated by interactions during foraging. All colonial spiders are orb-weavers. Individuals are aggregated in colonies that are formed by the individual capture webs attached together by means of communally built framelines (D'Andrea 1987; Avilés 1997; Uetz & Hieber 1997). The individual capture webs are the territories defended from other individuals within the colony. Spiders usually forage solitarily on their capture webs, although they can steal food from others. Individuals may benefit from an

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increase in individual food acquisition indirectly, as a consequence of web grouping, when insect prey that escape from one web are deflected onto others ('ricochet effect'; Uetz 1989) or by enabling spiders to take advantage of prey-rich web sites that are unavailable to solitary individuals (e.g. gaps between trees; Lubin 1974; Sandoval 1987). Group foraging is absent in most colonial species.

Web mechanics are the main argument proposed for the lack of group foraging in colonial species (Lubin 1974; Buskirk 1975a, b; Krafft 1979; Rypstra 1979). The poor communication of prey-induced web vibration is less effective across a colony consisting of individual webs than across a colony that constitutes a single, large capture web (Lubin 1974). Interestingly, colonial spiders that move between webs to capture prey and that show the greatest degree of group behaviour are those whose webs are joined to form continuous sheets (e.g. *Parawixia bistriata*: Fowler & Gobbi 1988; de Carvalho 1998).

Parawixia bistriata (Araneidae) individuals regularly engage in group capture and prey sharing. This species seems to have overcome the constraints imposed by the web to other colonial species and provides a unique opportunity to examine the features that may have allowed it to overcome these constraints. This species shows facultative group foraging. Individuals forage in groups only when the prey is larger than the spiders involved, otherwise they forage solitarily. This variability in capture behaviour may be facilitated by the fact that spiders can move quickly from one web to the next, because the orbs are placed within a single plane, forming an extensive sheet of capture webs.

The occurrence of group foraging can be affected by ecological factors such as the size of the prey items and the levels of prey available. First, the size of the prey can affect the likelihood of group capture by affecting the chances of monopolization of the item. Packer & Ruttan (1988) developed a series of models that incorporate payoffs to analyse the circumstances under which it is advantageous to forage collectively or solitarily depending on prey size. One of the predictions of the model is that, if a prey item is small enough to be monopolized by a single captor, the predator should capture prey solitarily. Because large prey items are difficult to monopolize, the occurrence of group capture could increase with prey size when the benefits of a joint capture outweigh the disadvantage of dividing the prey. These benefits can be represented by an increase in capture success or a decrease in the costs involved in the capture and subduing of a prey item: larger prey items can be riskier and more difficult to catch and demand more venom and enzyme investment to subdue and digest (Ward & Enders 1985).

A second factor that could affect the tendency of individuals to participate in group foraging is hunger level. Hunger stress increases the perceived value of a prey item and an individual's willingness to accept the risks and energy expenditure associated with prey capture (Riechert & Luczak 1982; Lubin & Henschel 1996; Ainsworth et al. 2002). Thus, in colonial spiders, hungrier individuals could show a higher tendency to attack prey, including items caught in a neighbour's web. For a resident spider, this can increase the investment in defence of prey

landing on its web. When residents try to maintain exclusive access to a prey item, it could result in aggressive interactions between neighbours. In addition, depending on the success of the resident spider at monopolizing the prey item, it could also result in more individuals participating in a capture (i.e. larger capture groups when prey is not monopolized by the resident spider).

I examined group prey capture behaviour of populations of *P. bistriata* from habitats with different resource levels. I compared the degree to which group foraging was related to food availability. I evaluated: (1) whether the strength of the tendency to forage in a group and the number of individuals participating in those groups increases with prey size and hunger stress; and (2) whether levels of aggression between the resident spider and neighbours participating in group foraging are higher in colonies under low prey conditions.

METHODS

Study Species

Parawixia bistriata (Araneidae) is a Neotropical colonial spider. Individuals defend their capture webs from conspecifics, but they also forage in groups, depending on the size of the prey (Fowler & Gobbi 1988; de Carvalho 1998). This species inhabits a diversity of habitats that vary in resource levels and thus constitutes a good system to examine the interaction between hunger stress and prey size on the occurrence of group foraging. Previous to this study, *P. bistriata*'s populations have been studied in the Cerrado habitat of Brazil, a tropical savanna-dry forest (Fowler & Diehl 1978; Gobbi et al. 1979; Sandoval 1987; Fowler & Gobbi 1988; de Carvalho 1998). Although these studies report the existence of facultative group-foraging behaviour in *P. bistriata*, no population comparison was made to examine the interaction between hunger level and prey size.

This univoltine spider is typically found in dry forests, but it also frequents a diverse range of habitats from semiarid scrub to wet forests in southeastern South America (Levi 1992). The development of these spiders 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 area, adults are found in the austral summer, at the end of December and January, and in the dry sites, adults are found in early autumn, between March and April.

The *P. bistriata* colony is composed of a communal retreat and thread framework built by siblings. The frame-lines forming this framework radiate from the retreat. The individual capture webs built on this framework form sheets of webs in a vertical position. When participating in group foraging, individuals can move across several webs to arrive at the web where the prey landed. There can be several planar sheets radiating from a retreat or from a nearby tree. This arrangement of webs differs from those of *Metopeira* species because web sheets are built in two dimensions and do not contain core and peripheral webs as is the case in *Metopeira* (Uetz & Hieber 1997; Rayor & Uetz 2000).

The spiders remain in the retreat during the day and move out onto the thread framework each night to build individual orb capture webs. These capture webs are consumed each day as individual spiders move back into the central retreat. There are, on average, 168 individuals per colony (range 14–914), although colony size varies depending on habitat type, with larger colonies in dry habitats (Fernández Campón 2005).

Colonies are started when adults disperse after moulting and subsequently begin to mate and lay egg sacs. This behaviour may be an adaptation to semiarid environments by frequently relocating the colony to suitable microclimates within these environments (Fowler & Diehl 1978; Fowler & Gobbi 1988).

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 of precipitation and the temporal variability in precipitation differ between 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 was in a provincial reserve, Guaycolec (26°10'S, 58°12'W); Wet 2 was in a private reserve, El Bagual (26°10'S, 58°56'W). The dry sites were near the town of Pampa del Infierno (26°30'S, 61°10'W) in Chaco province: Dry 1 was on the Allende family ranch 7 km northeast of Pampa del Infierno; Dry 2 was on a railroad right of way on the eastern side of town on public-owned land.

Climate and vegetation structure in dry and wet sites is compared in Fernández Campón (2005). 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 is lower in the dry sites. Mean \pm SE insect availability at the two wet sites during October 2001–January 2002 (measured as the insect dry biomass sampled by a Malaise trap per night: 0.28 ± 0.04 g) was almost twice that at the Dry 1 site (0.16 ± 0.02 g). I assumed that individuals in the dry sites were under stronger hunger stress than those in the wet sites. Thus, dry and wet habitat types represented my two levels of hunger stress.

Data Collection and Analysis

Occurrence of group feeding under natural conditions

I observed colonies of *P. bistrriata* in the field to estimate the natural occurrence of group feeding within a colony and compared these estimates between colonies from dry and wet habitats. Six and 16 colonies were sampled once in the dry and wet habitat types, respectively. These data were collected during my first field season, between

October 2001 and January 2002. The frequency of group feeding for a colony was calculated as the proportion of groups of spiders feeding relative to the total number of feeding events (solitary and groups) observed for that colony. I used the scan sampling method to obtain this estimate (Lehner 1996). The time it took to scan the complete sheet of joint webs varied with the size of the colony and the difficulty of assessing whether an individual (or group) was feeding. But, on average, it took 5 s to scan a linear metre of the sheet. Colonies were sampled at the beginning of the foraging activity period, within the first 2 h after the capture webs had been built.

The frequency data obtained from the observation of natural colonies permitted a Wilcoxon two-sample test comparison of the prevalence of group foraging in different habitats. I used the NPAR1WAY procedure in SAS, version 8.02, in the analysis (SAS 1999). To assess statistical significance, I used the *P* value obtained through a Monte Carlo method for the exact test because the sample size was small.

Effect of prey size on group foraging

I conducted a manipulative experiment to quantify the effect of prey size on the tendency to forage in groups. The experiment consisted of trials in which one prey item was offered to a spider positioned on its capture web. Observations were made using the focal animal method (Lehner 1996). Data were collected during two seasons: between October 2001 and January 2002, and between October 2002 and January 2003. I used moths as the prey item offered in the experiment, because insects from different orders vary in their profitability. Moths are also familiar prey to *P. bistrriata*. I collected the moths offered to the spiders at each study site using a light trap. Each moth was weighed with an Acculab field balance (model no. PP-2060D) prior to its release on the web.

The live moths were offered to spiders the night after being collected, or on some occasions, the second night after collection. Observations were made at dusk, once all the spiders in a colony had put up the webs (1930–2000 hours), and continued until there were no webs in the colony that met the requirements for sampling described below. I completed two to six trials at each colony.

When offered prey, the test spider was positioned on the hub of the capture web facing the ground. This is the standard foraging position shown by this sit-and-wait predator. A moth was offered to a spider by holding one of the anterior wings with forceps as it was placed on the web. Only trials in which moths fluttered their wings upon introduction were included in the analysis. All observations were made using a flashlight (covered by red cellophane to darken the light source, thereby reducing the light's attraction effect) and a 0-lx Sony handycam (model CCD-TR416).

Each prey item was placed on a web chosen haphazardly within a colony, with the following constraints: (1) the resident spider could not be feeding on a prey item at the time of release, (2) the resident was a sixth-instar individual and (3) at least four of the resident spider's nearest neighbours were positioned in foraging mode at the hubs of their webs. These criteria were followed under the assumptions

that spiders that were not feeding would be responsive to the prey item offered, and that by having spiders in the adjacent webs, there would be neighbours 'available' to participate in the capture and feeding of the prey item offered. In addition, because the response of individuals towards conspecifics and prey of different size can change with the developmental stage (de Carvalho 1998), I selected resident spiders of the same instar (sixth) in all trials to control for ontogenetic effects in foraging behaviour.

The sheets formed by connected capture webs usually expand from 0.5 m up to 3 m from the ground. I used a ladder to reach those capture webs located at the higher end of the sheet, but in some colonies, not all webs were accessible.

To examine how spiders share prey relative to the prey's size, I recorded the number of spiders participating in the capture of a given prey item, the maximum distance from which neighbour spiders came, 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 for at least 1 min during the feeding sequence, which ended with complete consumption or with the partitioning of the prey into pieces. The maximum distance from which neighbours joined the foraging group was measured as the number of webs separating the resident's web from that of the furthest neighbour. Webs surrounding the focal web (resident spider) were numbered in ascending order as distance from the focal web increased (i.e. web 1 was the closest to the focal web). Measuring the maximum distance from which neighbour spiders approach the foraging group in web units gives an idea of how many territories the spiders have to cross to join the foraging group in addition to the actual distance that the spiders traverse.

To control for differences in web size and distance of colonies from different habitat types, I compared the metric distances between the centre of a focal web (hub) to the six closest webs in different colonies from dry and wet sites to test for habitat differences. I sampled 11 colonies in dry sites (8 in Dry 1, 3 in Dry 2) and six colonies in the wet sites (8 in Wet 1, 2 in Wet 2).

I performed logistic regressions (GENMOD procedure in SAS) to examine the tendency for spiders to attack and feed collectively on prey relative to prey size. These analyses allowed me to explain how the frequency of group capture (or feeding) varies with the explanatory variables. The occurrence of group capture or feeding (both indicated as presence-absence) was the response variable in respective runs, and the variable prey size (mass of the prey item offered measured in grams) was used as a continuous explanatory variable. Year (first or second field season) and habitat (dry or wet) were the categorical explanatory variables.

To examine which variables influenced the size of a foraging group, I analysed the trials in which the prey item was captured or fed on by a group of individuals. In these analyses, group size (the number of spiders participating in the capture of or feeding on a prey item) was the response variable and, as with the logistic regression

models described above, prey mass, year and habitat were the explanatory variables. 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 generalized linear model with Poisson errors, a logit link function and type III significance tests (Poisson regression) to these data using PROC GENMOD in 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 χ^2 test (Stokes et al. 2000). In order to estimate how well the model explained variation in the response variable, adjusted R^2 were calculated for both logistic and Poisson regressions as suggested by Mittlböck & Waldhör (2000) using the log-likelihood estimates from the SAS output.

To test for habitat effects on the distance traversed by neighbours participating in the capture and feeding of a prey item, I performed a Poisson regression. This method was appropriate because values for the response variable (number of webs from focal web) were integers. The model included habitat, prey mass and the interaction effect as the explanatory variables and web distance as the response variable. The data were underdispersed, so I scaled them using the deviance to improve the fit to the model.

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.

An a posteriori estimate of interobserver reliability on the number of spiders participating in the capture of a prey was obtained by having two observers score the videotaped prey sequences for group size counts during the period of capture. I performed a Spearman rank correlation between the data taken by the two observers from the video. A limitation of this test for reliability is that, in the field, spiders can be counted more easily than from a video projected on a two-dimensional screen filmed from a fixed point. Thus, the estimates of interobserver reliability are probably an underestimation of the likely level of agreement between observers recording the data in the field. Interobserver reliability measured as the correlation between the number of spiders participating in the capture of a prey counted by two observers from videotaped trials was almost 90% (Spearman rank correlation: $r_s = 0.88$, $N = 15$, $P < 0.01$).

Interactions between the resident spider and neighbours during foraging

To examine interactions among spiders during foraging and to test for differences in agonistic interactions among

individuals of dry and wet habitats, I videotaped foraging trials as described above in the manipulative experiment and later completed a sequential analysis (Bakeman & Gottman 1997) of foraging behaviour for solitary individuals and groups from both habitat types. I analysed both group- and solitary-foraging events because I wanted to examine the existence of agonistic interactions during group foraging as well as the existence of behavioural differences in those events when the resident spider succeeded in monopolizing the prey (solitary foraging) and when it failed (group foraging) that could be affecting the result of the interaction (group or solitary foraging).

A trial started when I introduced the prey to the web of the resident spider and it ended when the resident spider was feeding alone either on the whole prey or on a piece of it. To record the occurrence of behavioural acts, I used the focal animal method (Lehner 1996) with the resident spider as the focal animal and I recorded all interactions between the resident spider and neighbour spiders. I analysed data on nine solitary- and nine group-foraging trials of each habitat type. I used individuals from different colonies in each trial except for two foraging trials in both dry and wet habitats that were conducted in the same colony and during the same night. However, because of the constraints for choosing a web for a trial (the resident spider and at least four neighbours could not be feeding), most of the individuals participating in a trial had not been involved in previous trials. Data were recorded using a 0-lx Sony handycam (model CCD-TR416). The mean \pm SE size of the prey items offered had a similar distribution both in the group trials (dry: 0.09 ± 0.02 g; wet: 0.09 ± 0.01 g; ANOVA: $F = 0.00$, $P = 0.99$) and in the solitary-foraging trials (dry: 0.07 ± 0.02 g; wet: 0.05 ± 0.01 g; $F_{1,16} = 0.81$, $P = 0.38$). The mean \pm SE number of spiders feeding on the prey items offered was 6.9 ± 3.1 in dry habitat and 5.0 ± 2.7 in wet habitat. The trials were recorded during the first field season from October 2001 to January 2002.

All occurrences of behavioural acts during group and solitary foraging were recorded using The Observer software, version 5.0.31 (Noldus Information Technology, Wageningen, The Netherlands). The behavioural acts recorded were based on those defined by Hodge & Uetz (1995) for agonistic encounters in colonial *Metepeira* and on other behaviours previously recorded for *P. bistriata* during foraging (Fernández Campón 2005). The list of behavioural acts is shown in Table 1.

To test for an effect of habitat in the frequencies of those behavioural interactions between the resident spider and the other individuals in the foraging group, I performed a one-way ANOVA (Table 1) with habitat as a factor. I used the ranks of the frequencies because the data did not show a normal distribution.

To develop a pathway diagram to describe the sequences of behaviour involved in foraging, frequencies of behavioural transitions were input into matrices produced by The Observer software. In these matrices, behavioural acts appearing in rows represented the preceding behaviour and behavioural acts in columns represented the target or subsequent behaviour. The transition matrices were summed over all individuals from the same habitat of origin. The

summed matrices were used to calculate adjusted residuals (adjusted residuals represent the difference between the observed and the expected values for the transition frequency). The distribution of the adjusted residuals is expressed according to a Z distribution. I developed path diagrams representing behavioural sequences using the adjusted residuals of behavioural transitions (Van den Berg et al. 1999). I used only positive adjusted residuals to identify transitions that occurred more often than expected according to random distribution (Figs 3 and 4). In addition, to detect differences between groups of individuals from different habitats, means \pm SE of the adjusted residuals were calculated for selected transitions and analysed using Student's t test. Only trials in which the transition of interest occurred were included in the analysis (i.e. trials in which the frequency was zero were not included).

To examine the effect of prey size on spider interactions, I performed a sequential analysis on the group-foraging trials described above but, in this case, discriminating between trials in which the three smallest prey items (mean \pm SE size: dry: 0.05 ± 0.03 g; wet: 0.06 ± 0.01 g; ANOVA: $F_{1,4} = 0.20$, $P = 0.67$) and the three largest prey items (dry: 0.14 ± 0.02 g; wet: 0.12 ± 0.03 g; $F_{1,4} = 0.64$, $P = 0.47$) were offered to individuals from dry and wet habitats. The mean \pm SE size of foraging groups from dry and wet habitats was as follows: dry habitat: small prey, 7.0 ± 1.0 ; large prey, 6.0 ± 1.7 ; wet habitat: small prey, 3.7 ± 1.2 ; large prey, 3.7 ± 1.5 . I also performed the same analysis for solitary-foraging trials, comparing the behavioural sequence of the three trials with the smallest prey and largest prey for individuals from dry and wet habitats. The size of the prey item offered within each size category was similar between habitats (small prey trials: $F_{1,4} = 0.16$, $P = 0.71$; large prey trials: $F_{1,4} = 0.10$, $P = 0.77$). Tables showing the transitional probabilities matrices for each data set are included as Supplementary Material (Tables S1–S8).

RESULTS

Occurrence of Group Feeding Under Natural Conditions

Group feeding events occurred in 31% of all the colonies sampled in the wet sites ($N = 16$) and 83% of colonies sampled in the dry site ($N = 6$). Within colonies with group foraging, the proportion of group feeding relative to the total number of feeding events was similar between habitats (Wilcoxon two-sample exact test: $S = 87.50$, $Z = 1.45$, $P = 0.15$). While approximately 5% of all feeding events in these colonies corresponded to feeding groups, 26% of all individuals feeding at one time were participating in group feeding. There was no correlation between the total number of individuals that joined a feeding group and the total number of individuals within the colony (Spearman rank correlation: $r_s = 0.30$, $N = 9$, $P = 0.42$). The lack of a correlation could be due to the small sample size and the presence of an outlier. The deletion of one observation from the dry site increased the strength of the correlation ($r_s = 0.68$, $N = 8$, $P = 0.06$).

Table 1. List of behavioural acts performed by *P. bistriata* in foraging trials and used in sequential analysis (see text for explanation)

Interaction with	Behavioural act	Definition	Aggression rank
Prey	Bite	Bites the whole prey with chelicerae or has the mouth on prey as if feeding from it	—
	Cuts Lines	Cuts the thread lines that attach the prey item to the web	—
	Eat Piece	Eats a piece of the prey that has been previously pulled from the whole prey	—
	Pluck Web	Pulling web radii towards body. Web-plucking movements usually done by a spider when prey enter a web	—
	Prey Escapes	Prey drops or flies away from the capture web	—
	Pull Prey	Pulls at prey either to get a piece or to take it elsewhere	—
	Wrap Prey	Wraps prey with silk using legs III & IV	—
Prey/neighbour	Approach	Moving towards the prey or neighbour	0
	Focus	Orientation of the body towards the prey or a neighbour	0
	Freeze	Sudden cessation of movement in response to a movement/vibration	0
	Look Place	Walks on prey or on other group-feeding spiders as if looking for a place to feed on prey	0
	Walks Away	Walks away from prey item or neighbour spider	0
Neighbour	Grapple	Grapples with another spider using the legs. No bites involved	2
	Leg Contact	Touches another spider with first pair of legs	0
	Shake Web	Shakes web using front pair of legs. Usually performed in response to vibration produced by another spider, sometimes orientating the body towards the other spider	1

Effect of Prey Size on the Tendency to Attack and Feed on Prey as a Group

Group prey capture increased with prey size (Table 2). In addition, individuals from dry habitats were more likely to capture prey as a group than were individuals from populations residing in wet habitats, regardless of prey size (chi-square test: $\chi^2_1 = 5.28$, $P = 0.02$, $\beta_{\text{dry vs wet}} = 0.56$, odds ratio = 1.75; Fig. 1a), but no significant differences were found between years.

Similar to the occurrence of group capture, individuals were more prone to feed in a group when larger prey were offered ($\chi^2_1 = 48.08$, $P < 0.01$). However, in this case, there were no differences between years ($\chi^2_1 = 2.99$, $P = 0.08$) or between habitats ($\chi^2_1 = 1.22$, $P = 0.27$; Fig. 1b).

Neither the date nor the time of the trial was correlated with the size of the prey offered (Spearman rank correlation: date: $r_s = 0.10$, $N = 319$, $P = 0.08$; time: $r_s = -0.06$,

$N = 314$, $P = 0.29$). The absence of a correlation allowed rejection of any effect of these temporal variables on the response of the spiders.

Effect of Prey Size on Group Size during Capture and Feeding

The number of spiders participating in a capture group increased with prey size (Table 2, Fig. 2). This increase in group size was higher for individuals from dry habitats than for individuals from wet habitats (prey mass*habitat type: $\chi^2_1 = 4.79$, $P = 0.03$, $\beta_{\text{dry vs wet}} = 1.10$, predictor value = 3.00; Fig. 2a, b). The size of the feeding groups showed the same trend: the number of feeders present in a group corresponded to prey size (Table 2). However, habitat differences were more pronounced for feeding groups than they were for capture groups, as indicated

Table 2. Generalized linear model analyses of the group-foraging variables examined in *P. bistriata* individuals from dry and wet habitats

Response variable modelled	Explanatory variables	df	χ^2	P	Deviance (df)	R^2_{adj}
Frequency of group capture trials	Prey mass (g)	1	25.30	<0.01	395.10 (314)	0.87
	Habitat	1	5.28	0.02		
	Year	1	0.26	0.61		
Size of capture groups	Prey mass (g)	1	13.47	<0.01	46.73 (125)	0.98
	Habitat	1	0.12	0.73		
	Year	1	1.35	0.24		
	Prey mass*habitat	1	4.79	0.03		
Size of feeding groups	Prey mass	1	14.43	<0.01	148.82 (127)	0.90
	Habitat	1	0.00	0.99		
	Year	1	6.37	0.01		
	Prey mass*habitat	1	11.47	<0.01		

Frequency data (number of group trials/number of solitary trials) were analysed using a binomial distribution of errors; group size data (number of spiders participating in capture or feeding groups) were modelled with Poisson distribution of errors.

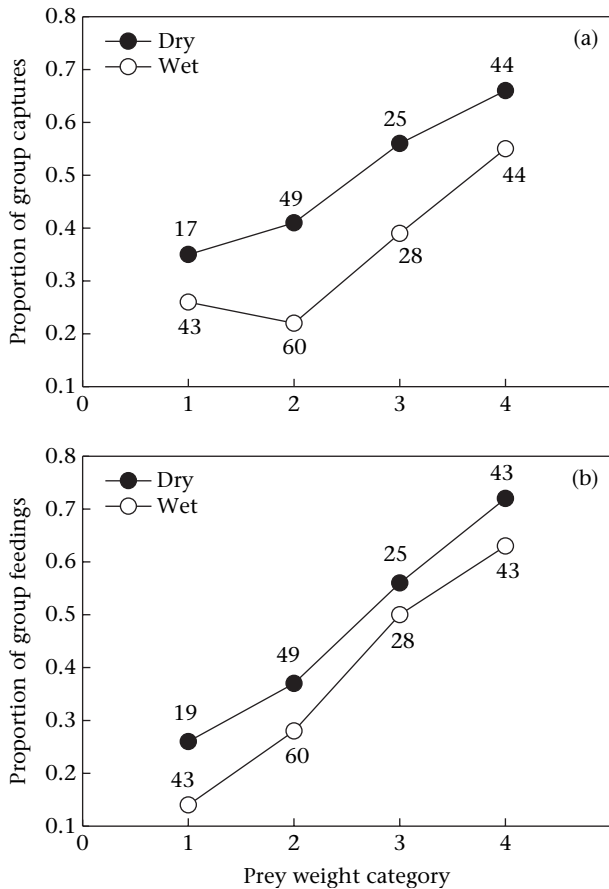


Figure 1. Proportion of collective (a) captures and (b) feeding events by *P. bistriata* as a function of prey size in dry and wet habitats (inset values = number of trials per prey size class). Prey sizes are pooled for presentation into four categories, each representing a percentage of the mean \pm SE mass of a sixth-instar spider (0.196 ± 0.005 g, $N = 215$): 1 = 0–25%; 2 = 25.1–50%; 3 = 50.1–75%; 4 > 75%.

by a larger β ($\chi^2_1 = 11.47$, $P < 0.01$, $\beta_{\text{dry vs wet}} = 1.73$, predictor value = 5.62; Fig. 2c, d). There were also differences in the size of the feeding groups between years. However, the responses of individuals occupying dry versus wet habitats did not differ between seasons (dry_{2nd vs 1st season}: $\chi^2_1 = 3.02$, $P = 0.08$; wet_{2nd vs 1st season}: $\chi^2_1 = 1.02$, $P = 0.31$), indicating that between-season variation did not cause habitat differences.

The distance (measured in number of webs) traversed by neighbours joining a capture was similar between habitat types (GLM: $F_{1,66} = 0.00$, $P = 0.95$); only the size of the prey affected this distance ($F_{1,66} = 32.17$, $P < 0.01$). In contrast, both prey size and habitat had a significant effect on the distance traversed by neighbours participating in feeding groups (prey size: $F_{1,81} = 14.05$, $P < 0.01$; habitat: $F_{1,81} = 14.85$, $P < 0.01$), but the interaction between these two variables was not significant ($F_{1,81} = 3.63$, $P = 0.06$). Neighbour spiders that participated in feeding groups in the dry habitat came from more distant webs than spiders in wet habitat (median (25–75% quartiles); dry: 2 (1–3); wet: 1 (1–2)). The distance between webs within a colony (estimated as the distance between a focal web and the six adjacent webs) was similar between habitats (Table 3).

Interactions between the Resident Spider and Neighbours during Foraging

Sequential analysis results of the trials with group-feeding events revealed that behavioural sequences differed when individuals representing a given habitat type foraged on small versus large prey items (Fig. 3). Behavioural acts reflecting high levels of aggressiveness (Table 1), such as Shake Web and Grapple, occurred between the focal and neighbouring spiders from dry sites when foraging on small prey but not when foraging on large prey (contrast Fig. 3a, b). Note that in trials with small prey items, the behavioural sequence was Leg Contact–Grapple–Eat Piece. However, in order for the focal individual to eat a piece of prey, it should have pulled it from the prey first. Pull Prey was not always noticed in the trials when Grapple occurred because grappling in those sequences quickly followed Pull Prey. Thus, the main difference between foraging groups from dry habitats feeding on small versus large prey items was in the occurrence of grappling behaviour followed by the monopoly of the piece of prey by the focal individual in the case of the smaller prey items.

In trials with individuals from wet habitat, there were no behavioural acts with high levels of aggression and the main difference between trials with prey of different sizes was in the occurrence of behavioural acts in which spiders were in direct contact (Fig. 3c, d). Social interactions such as leg contact occurred only when foraging on small prey. In trials with large prey, the sequence mainly involved looking for a place on the prey item to feed and some prey-wrapping behaviour, but there was no direct contact between individuals that were feeding. This finding could reflect the small number of individuals noted for foraging groups in the wet habitat. The size of the large prey items offered was twice the size of a sixth-instar spider (mean \pm SE body length: prey items offered = 20.18 ± 0.81 mm, $N = 6$; sixth-instar spider = 9.87 ± 0.1 mm, $N = 113$). Thus, the chances of being close to another individual when foraging on a large prey might not be as high when fewer individuals are feeding (unless individuals purposely forage in close contact).

In solitary-foraging trials, neither the size of the prey nor the habitat had an important effect on the average frequency of behavioural acts (Table 4) or the behavioural sequence (Fig. 4a, b). The behavioural sequence in solitary trials contained a subset of behaviours that occurred during group foraging (Fig. 4c, d).

Among group-foraging trials, there was no habitat effect on the average frequency of behaviours involving interactions between the resident and neighbour spiders (Table 5). Only the difference in frequency of Leg Contact approached significance, despite high variability among trials in the same habitat (ANOVA: $F_{1,16} = 4.37$, $P = 0.05$; mean \pm SD Leg Contact: dry: 17.22 ± 13.59 ; wet: 6.88 ± 6.67). When comparing behavioural transitions, Bite–Leg Contact was significantly more frequent in trials with individuals from dry habitat (Student's *t* test: $t_{15} = 3.31$, $P < 0.05$), while the transitions Bite–Look Place and Leg Contact–Pull Prey were significantly less frequent in those trials ($t_{15} = -2.44$, $P < 0.05$; $t_{14} = 2.18$, $P < 0.05$).

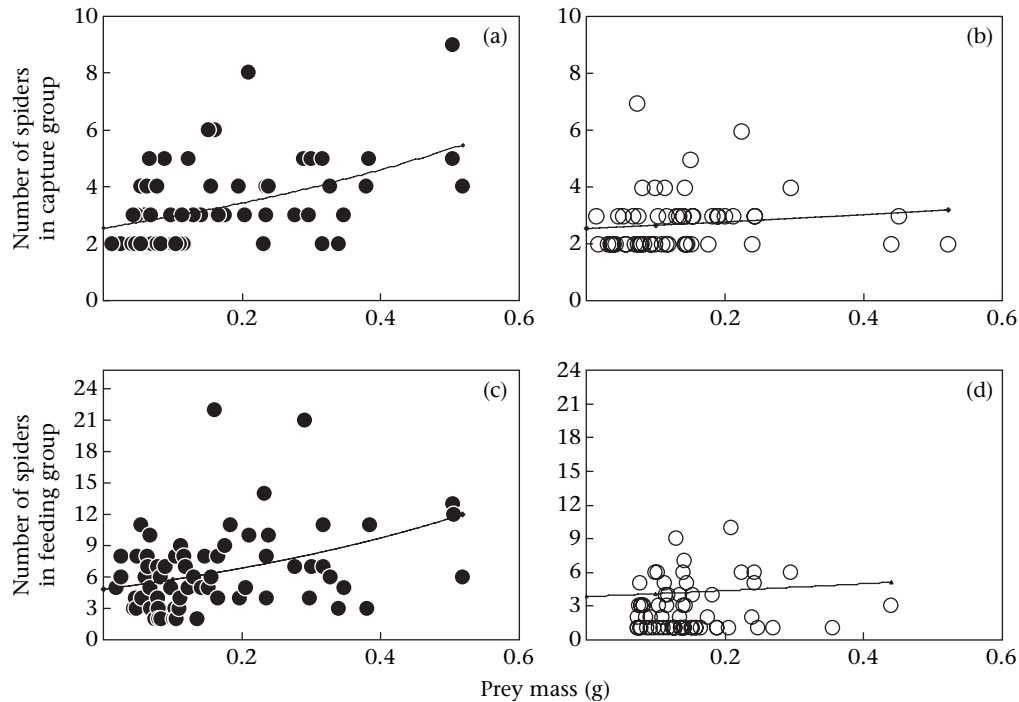


Figure 2. Number of *P. bistriata* participating in group capture and feeding of prey as a function of prey size. Regressions are based on estimates for a Poisson distribution (Table 2): (a) capture group from dry habitat, $Y = e^{(0.9204+1.4723X)}$; (b) capture group from wet habitat, $Y = e^{(0.9408+0.4387X)}$; (c) feeding group from dry habitat, $Y = e^{(1.5759+1.7524X)}$; (d) feeding group from wet habitat, $Y = e^{(1.3497+0.6514X)}$.

In solitary-foraging trials, the behavioural transition Shake Web–Shake Web was significantly more frequent in trials with individuals from dry habitat than it was in trials with individuals from wet habitat ($t_{11} = 3.31$, $P < 0.05$). In contrast, the transition Bite Prey–Wrap Prey was significantly less frequent in trials with individuals from dry habitat ($t_{14} = -2.85$, $P < 0.05$). There were no differences between habitats for any of the other behavioural transitions.

DISCUSSION

Of all aspects of foraging behaviour studied here, the tendency to attack prey in a group and the sizes of the capture and feeding groups differed between the two habitat types. The consequences of these behavioural differences are that spiders from dry sites can potentially increase the amount of food they consume. Through group capture of large prey, individuals can feed more often and on more prey, which would not be available when group foraging does not occur. In addition, compared to solitary catches, the amount of food coming from the large prey consumed collectively is spread among more members of the colony. This allocation of food can have an important effect on growth and survival of individuals in drier habitats with lower prey levels.

Despite differences in prey availability, field observations showed that, within colonies, the occurrence of group feeding was similar in dry and wet habitats. Relative to the solitary-feeding events, group-feeding events in the field were low, but 26% of the individuals in the colony

that were feeding at one time were found in feeding groups. However, when considering all colonies sampled in each habitat type (and not only colonies in which group feeding was recorded), the proportion of individuals participating in group feeding was higher in dry habitats, because group foraging occurred in most of the colonies sampled. In addition, in colonies from the dry sites, individuals showed a higher tendency to capture prey in groups and there were more individuals participating in both capture and feeding groups, with individuals in feeding groups traversing longer distances in the dry sites.

The stronger response of individuals from dry habitats, shown as a higher tendency to forage in a group and more individuals in those groups, can result from the higher hunger levels experienced. High hunger levels can, in turn, increase the perceived benefits of a collectively captured prey for neighbours but increase prey defensibility costs for

Table 3. General mixed model ANOVA of the distance from a focal *P. bistriata* web to the six closest webs in dry and wet sites

Source	df		F	P
	Numerator	Denominator		
Adjacent web no.	5	394	21.34	<0.01
Habitat	1	1.93	0.12	0.76
Habitat*adjacent web no.	5	394	0.12	0.99

Covariance parameter estimates: site (habitat) = 24.09; residual = 164.39.

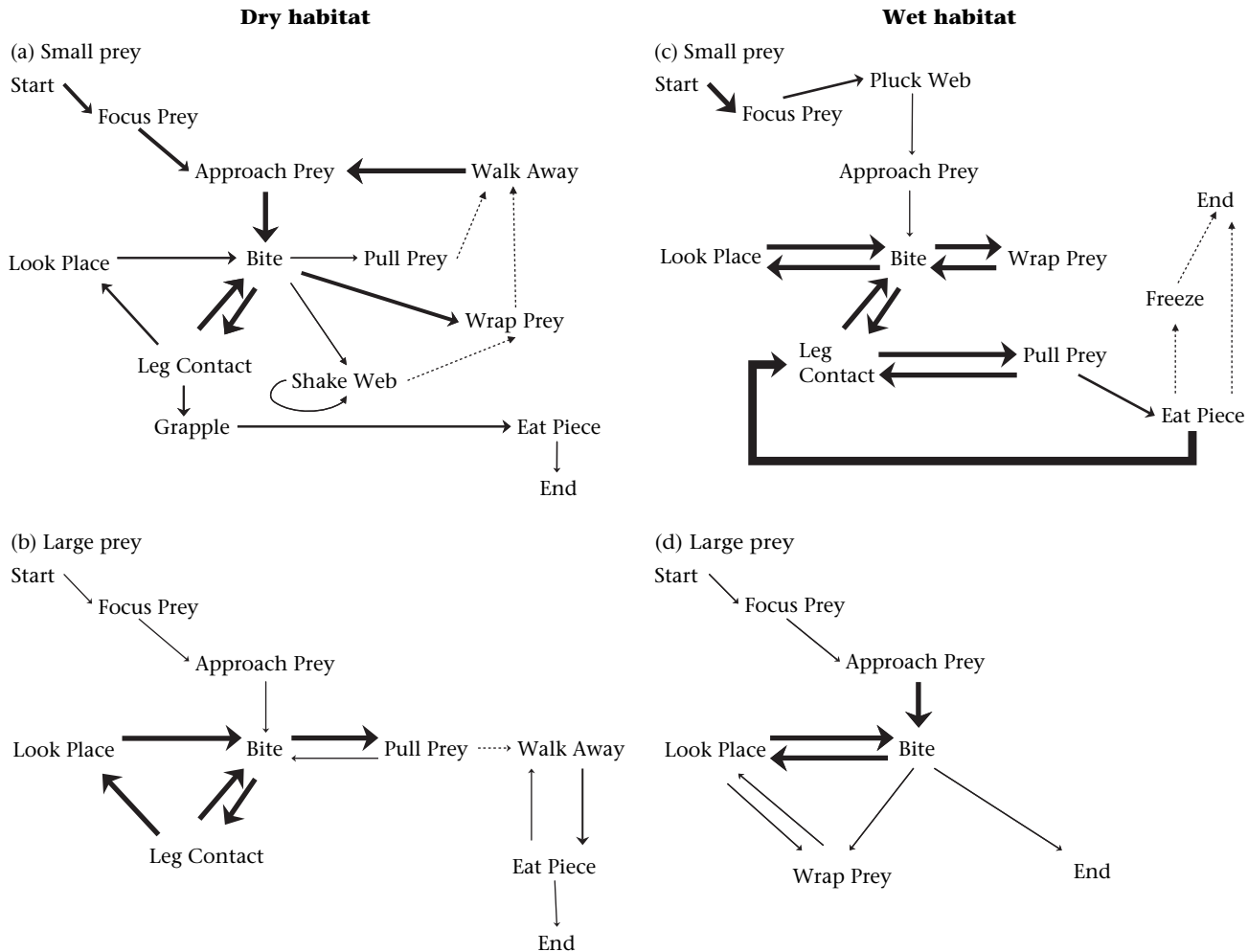


Figure 3. Behavioural sequences during group-foraging trials in which *P. bistriata* from (a, b) dry habitats and (c, d) wet habitats were offered small prey and large prey, respectively. Solid arrows depict significant behavioural transitions; the thickness of the arrow refers to the value of the adjusted residual (*Z*) in the transition matrix (thin arrows: $Z > 1.96$, $P < 0.05$; medium arrows: $Z > 2.58$, $P < 0.01$; thick arrows: $Z > 3.29$, $P < 0.001$). Dotted arrows indicate nonsignificant transitions used to complete the sequences, based on the highest transition probabilities. See Table 1 for behavioural act descriptions.

the resident. Hunger levels affect individual aggressiveness (Riechert 1979, 1998) and willingness to accept higher risks and energy expenditure associated with capture of a prey that would otherwise be ignored (Riechert & Luczak 1982; Lubin & Henschel 1996; Ainsworth et al. 2002). Although spiders from dry habitats should be more tenacious at

defending their webs and the prey landing on them (Riechert 1978, 1991; Uetz et al. 1982; Uetz & Hodge 1990), it is possible that the high prevalence of group capture results from a stronger pressure on the part of the neighbours under low prey levels compared to populations under higher prey levels.

Table 4. Two-way ANOVA of ranked frequencies of behaviours occurring in all types of foraging trials with individual *P. bistriata* from dry and wet habitats

Behaviour	Source	<i>df</i>		<i>F</i>	<i>P</i>
		Numerator	Denominator		
Shake Web	Foraging mode	1	32	3.33	0.08
	Habitat	1	32	0.67	0.42
	Foraging mode*habitat	1	32	0.64	0.43
Wrap Prey	Foraging mode	1	32	3.72	0.06
	Habitat	1	32	0.02	0.88
	Foraging mode*habitat	1	32	1.05	0.31

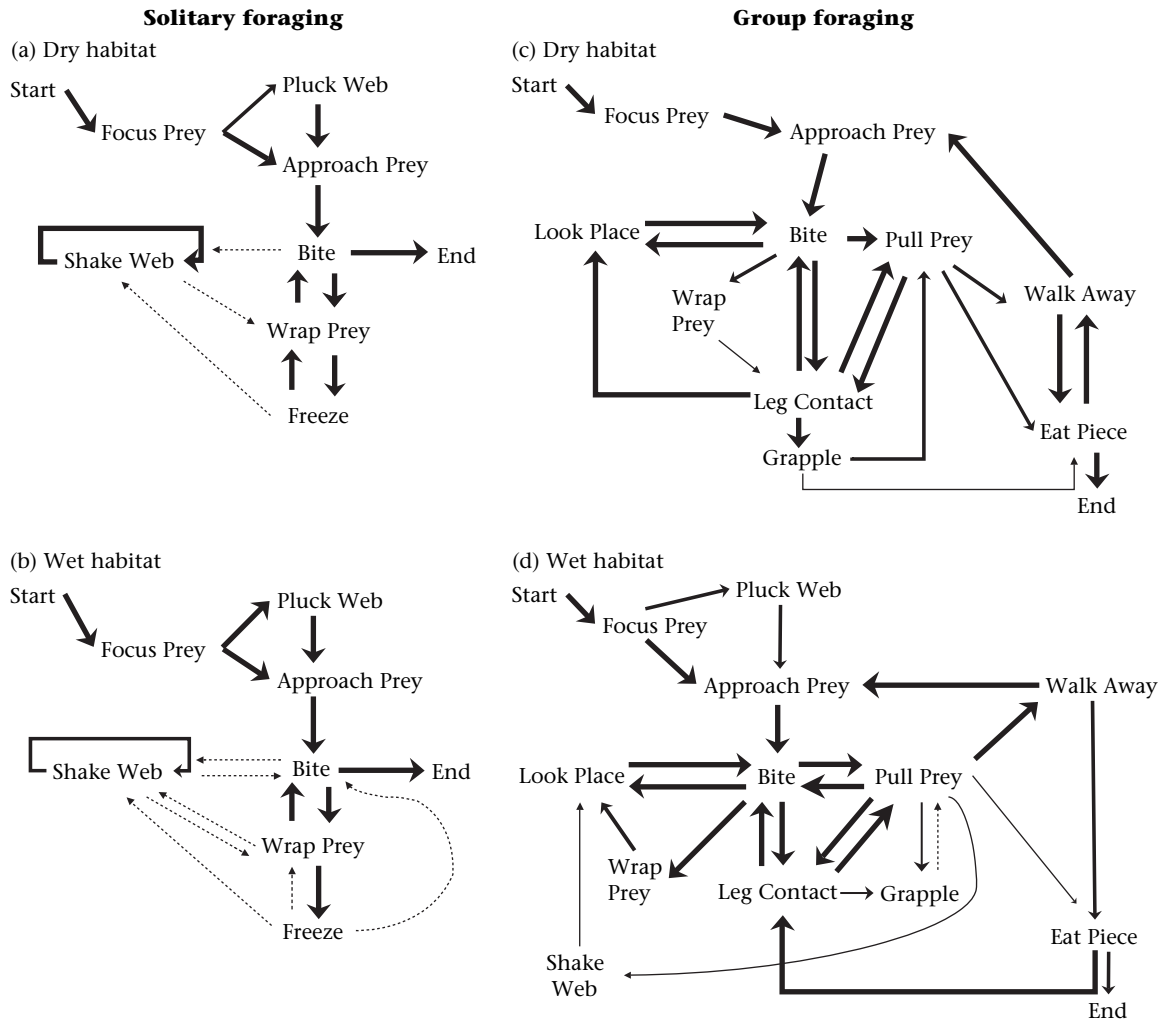


Figure 4. Behavioural sequence during (a, b) solitary-foraging trials and (c, d) group-foraging trials in which *P. bistriata* from dry and wet habitats, respectively, were offered all prey sizes combined. Conventions as in Fig. 3.

The pressure exerted by neighbours was evident in behavioural acts of residents, such as repetitive web shaking, which served as a rejection signal to neighbours. This type of behaviour was more frequent in solitary-foraging trials with individuals from dry sites. In addition, the preliminary analysis of group-foraging trials with small and large prey items showed that resident spiders from dry habitats feeding on small prey items also signal to neighbours with web shaking. In these trials, grappling

followed the monopoly of a piece of prey by the resident spider. When feeding on larger prey, however, behavioural acts did not escalate to grappling, probably because of the impossibility of defending the prey item. But other social interactions, such as leg contact following prey biting, were more frequent overall in group foraging trials with individuals from dry habitats than in those with individuals from wet habitats feeding on large prey. In these individuals, other behaviours that do not involve direct

Table 5. One-way ANOVA of ranked frequencies of behavioural acts performed by *P. bistriata* in group-foraging trials and the proportion of trials in which the particular behavioural acts occurred

Behavioural act	df		F	P	Proportion of trials in which behaviour occurred	
	Numerator	Denominator			Dry habitat	Wet habitat
Leg Contact	1	16	4.37	0.05	1.00	0.89
Shake Web	1	16	1.41	0.25	0.56	0.33
Grapple	1	16	1.15	0.30	0.67	0.33

contact between the resident and neighbour spiders (e.g. looking for a place to feed on the prey or pulling from the prey) were more frequent when feeding in a group. Thus, prey defensibility seems to be affected by neighbour pressure, particularly under low prey levels. The defence cost incurred over a large prey may be too high for a resident, because large prey are capable of producing vibrations that attract several distant neighbours. Residents simply may be unable to stop the influx of other members of the colony (de Carvalho 1998).

In this respect, group foraging in *P. bistrata* seems similar to cases of food parasitism or joining (sensu Giraldeau & Beauchamp 1999), something that has been widely reported in fish (e.g. giant danio fish, *Danio aequipinnatus*; zebrafish, *Danio rerio*: Chapman & Kramer 1996) and birds (e.g. house sparrows, *Passer domesticus*: Johnson et al. 2004). True cooperative foraging involves active recruitment to a food source, something commonly observed in termites and the social Hymenoptera. It has even been reported for lepidopteran larvae (Fitzgerald & Peterson 1988). In groups of foraging fish and birds, food defence and aggressive interactions are modulated by the size of the food item and the number of individuals in the group, as observed in this study for *P. bistrata*.

Group foraging in *P. bistrata* allows an individual under conditions of low resources to gain access to prey caught outside its capture web, its feeding territory. By intruding on the foraging bouts of neighbours, a significant proportion of individuals within a colony can profit from prey caught on webs other than their own. This strategy may also benefit the resident spider because individuals tend to have a lower capture success with larger prey that, aside from merely escaping, can inflict injury to the spider. Studies specifically completed on other cooperative and colonial species indicate that capture success of large prey by an individual spider is lower than that by a group (*Anelosimus eximius*: Nentwig 1985; *Stegodyphus mimosarum*: Ward & Enders 1985; *Philoponella republicana*: Binford & Rypstra 1992) and subduing and consuming these large prey may demand the investment of a significant amount of energy (Ward & Enders 1985). Moreover, the relative benefits of group capture and feeding are even greater if solitary individuals cannot fully consume large prey that have required considerable investment in venom and silk to subdue (Rypstra & Tiley 1991).

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Supplementary Material

Supplementary material for this article can be found, in the online version, at doi:10.1016/j.anbehav.2007.02.030.

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