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I am submitting herewith a dissertation written by María Florencia Fernández Campón entitled “Variation in life history and behavioral traits in the colonial spider *Parawixia bistriata* (Araneidae): some adaptive responses to different environments”. I have examined the final electronic copy of this dissertation for form and content and recommend that it is accepted in partial fulfillment of the requirement for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

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VARIATION IN LIFE HISTORY AND BEHAVIORAL TRAITS IN THE COLONIAL SPIDER *Parawixia bistriata* (ARANEIDAE): SOME ADAPTIVE RESPONSES TO DIFFERENT ENVIRONMENTS

A Dissertation
Presented for the
Doctor of Philosophy Degree

The University of Tennessee, Knoxville

María Florencia Fernández Campón
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To my family.

To my parents, Josefina Vicente and Carlos Fernández Campón, and my sister María Sol. I thank them for their constant support.

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ABSTRACT

Widely distributed species are exposed to different environmental forces throughout their range. As a response to differences in local environmental conditions, these species are expected to present geographic variation in phenotypic traits (e.g., behavioral, physiological, anatomical) in order to better adapt to these conditions. *Parawixia bistriata* (Araneidae) is a colonial spider distributed in a variety of habitats in South America. This species is unusual in two respects: contrary to most social species found in tropical wet forests, *P. bistriata*'s distribution extends from tropical to temperate latitudes; and it exhibits facultative group foraging, a behavioral pattern absent in territorial colonial spiders. In this dissertation, I examined the existence of geographic variation in life history and behavioral traits of *P. bistriata*'s populations inhabiting sites with distinctive environmental conditions and estimated success of populations. I performed reciprocal transplants of colonies to evaluate the influence of genetic and environmental forces on the variation exhibited in both life history and behavioral traits in populations from different habitats. When examining behavioral traits, I focused on foraging behavior as I wished to evaluate whether the expression of this behavioral pattern could explain the success of populations in diverse habitats types. Phenology of populations from the different habitats was out of phase. The differences exhibited in the phenology were a response of juvenile developmental traits to resources levels and possibly climatic factors such as temperature. Populations from the different habitats were equally successful as judged by the reproductive output of individuals and by the size of colonies. Data from the reciprocal transplants, however, suggested that populations constituted ecotypes: while individuals from dry habitat origin were successful in both native and foreign habitat, individuals of a wet habitat origin failed at reproduction in the foreign habitat. Analysis of foraging behavior showed that while some of the behavioral aspects that differed geographically exhibited plasticity, others, such as the tendency to capture and feed on prey as a group, exhibited divergence between populations from the different habitats. Individuals from populations with low resources exhibited plasticity for this trait: they tended to capture prey and feed as a group when resources are low, but solitarily when prey levels are high. On the other

hand, individuals from high resource habitats did not change between solitary and group foraging in response to different prey levels. The correspondence between reproductive effort and plasticity in group foraging suggests that the expression of this behavior is in part responsible for the success of populations of *P. bistriata* in habitats with low resources.

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Part I.

Introduction to sociality in spiders

ABSTRACT

Taxonomic groups that exhibit a diversity of social structures are particularly useful for examining the factors that influence the evolution of social behavior. Spiders characteristically exhibit high levels of aggression and cannibalism, but a variety of social structures (e.g., maternal-social group, cooperative and colonial species) are found and these are scattered among a number of taxonomic families. Web architecture appears to limit the degree of sociality exhibited by orb weavers: the highest level of sociality observed in this group is coloniality. Nevertheless, different levels of sociality exist in the orb weavers, and there is evidence for group foraging that would not be expected for a colonial system. *Parawixia bistriata* (Araneidae) is a widespread orb-weaving species that shows facultative group foraging. Previous studies of this species concentrated on populations in a semi-arid habitat but populations present in more mesic habitats could exhibit different behavioral and life history phenotypes in response to different local environments. This chapter is a review of social systems in spiders with particular reference to colonial species. It serves as an introduction to my analysis of the geographic variation in life history and behavioral traits of *P. bistriata.* In subsequent chapters I consider phenotypic responses to two environments and how such responses adapt this spider to the diversity of habitats in which it is found.

INTRODUCTION

Social species are those in which individuals form groups that are organized in a cooperative manner (Wilson 1978). Though most attention has been paid to social systems in hymenopteran insects (e.g., ants, honey bees, polistine wasps, Wilson 1971; Jeanne 1980; Hölldobler & Wilson 1990; Ross & Matthews 1991; Îto 1993), mammals (e.g., fossorial rodents such as naked and common mole-rats, Rodentia, Bathyergidae, Sherman et al. 1991; Burda et al. 2000) and birds (Stacey & Koenig 1990), cooperative behavior is widespread and has even been attributed to microorganisms (Strassmann et al. 2000). Taxonomic groups such as families or genera that contain species exhibiting different levels of sociality are particularly useful for comparative studies of social evolution. These studies can shed light on the evolutionary history of sociality within a

group and serve to identify the ecological, demographic, and genetic forces that drive or facilitate the origin of sociality.

Ecological factors such as predation (Schwarz et al. 1998), resource availability (Lacey & Sherman 1991; Creel 1997), and abiotic conditions (Soucy & Danforth 2002), can contribute to the evolution of sociality. Consequently, phylogenetically distant taxa with very different life history characteristics may show similar behavioral adaptations in response to ecological factors. For example, polistine wasps and cooperatively breeding vertebrates both have social groups consisting of conspecific adults living together and cooperating as helpers in the rearing of non-descendant young. Brockmann (1997) suggests that this convergence in social behavior reflects, in part at least, an adaptive response to high costs of independent reproduction. On the other hand, closely related species and even populations of a species may show divergence in social structure reflecting the different environmental selection pressures they have encountered. The obligately eusocial wasp from Europe, *Lasioglossum malachurum* (Hymenoptera, Halictidae), for instance, generally exhibits a eusocial structure with geographic variation in colony size in a north-south cline in response to abiotic conditions. Departure from eusociality, however, occurs at lower latitude sites with workers taking on a reproductive function after the colony's queen has died. Richards (2000) cites the extended breeding season experienced at lower latitudes as contributing to this shift from eusociality in local populations of *L. malachurum*.

The arachnid order Araneae is a particularly interesting group from the standpoint of social structure. The vast majority of the almost 39,000 described species in this order are aggressive and solitary (Platnick 2005). Social species constitute 0.1% of the species in the order and there is considerable diversity in the levels of sociality exhibited among these species (Buskirk 1981; D'Andrea 1987; Riechert & Roeloffs 1993). This provides an excellent opportunity for studying the evolution of sociality in a system in which selection pressures have overcome basic aggressive tendencies.

Most social species of spiders are found in wet tropical areas (Riechert 1985). Resource levels at those habitats are thought to be sufficiently high as to lead to a shift towards higher tolerance among conspecifics. Greater tolerance might have in turn

facilitated the evolution of social species of spiders (Rypstra 1986). Yet there are some species that are found in more xeric habitats such as social members of the genus *Stegodyphus* (Eresidae; hackled-band weaver) that inhabit African savanna and the south American orb-weaver, *Parawixia bistriata* (Araneidae). Although *P. bistriata* is commonly found in semi-arid habitats, it also occupies more mesic areas. Due to its widespread distribution, *P. bistriata* represents a good model species for studying life history and behavioral adaptations to the environmental conditions found in the different habitats it occupies. I am particularly interested in examining variation in those social foraging traits that may have allowed *P. bistriata* to colonize habitats offering different resource levels.

In this introductory part of the thesis I review the characteristics that spiders share with other social arthropods and describe the different social systems found in spiders with an emphasis on colonial species, a classification assigned to *P. bistriata*. I also review the literature on *P. bistriata*, in particular, information on its life-history and social behavior. In chapters II to IV, I test for ecotypic variation in a relevant set of life history and social traits in this species.

PREDISPOSITION TO SOCIALITY: CONVERGENCE WITH OTHER TAXA

The use of silk or silk-like secretions in nest construction (Crespi & Choe 1997) is a convergent trait shared by spiders, other social arachnids (i.e., mites, Acari) and many social insects (i.e., web spinners [Insecta, Embidiina], book-lice [Insecta, Psocoptera], and lepidopteran larvae [Insecta, Lepidoptera]; Fig. 1). Silk is expensive to produce (Riechert 1985; Uetz & Hieber 1997), but Riechert (1985) has shown that social spider groups require less silk *per capita* than would be required of the solitary spider. Thus, cooperation in nest building and maintenance can reduce nest and web trap production costs.

The nest is extremely important to a colony as it serves as a protective structure against predators and parasites (Acari, Saito 1997; Embiidina, Edgerly 1997; Psocoptera, New 1973 in Edgerly 1997), and can also help in thermoregulation and foraging (lepidopteran larvae, Fitzgerald & Peterson 1988; Costa & Pierce 1997; spiders, Avilés

1997). Silk in the structure also facilitates communication among group members in spiders as it serves as a substrate for the transfer of vibratory signals.

Further support for the idea that the use of silk is an important trait in the evolution of sociality in spiders comes from social species that belong to non web-building spider families. These vagrant (wandering) and ambush spiders include crab (Thomisidae), wolf (Lycosidae), fishing (Pisauridae), lynx (Oxyopidae) and jumping (Salticidae) spiders families. Most species in these groups do not build web traps though they may have silk-lined burrow or sac-shaped retreats in which they harbor when inactive. Social representatives of these non-web-builders have an extended retreat that serves a secondary function, prey capture (the genus *Diaea*, Thomisidae; Evans 1998; Evans & Goodisman 2002, and undescribed lynx spider species of the genus *Tapinillus*, Oxyopidae ; Avilés 1994). The lynx spider representatives even has a distinct web trap (Avilés et al. 2001).

CLASSIFICATION OF SOCIAL SYSTEMS IN SPIDERS

Social behavior in spiders ranges from temporary aggregations of individual webs to permanent web colonies containing thousands of individuals in which there is cooperative care of the brood (Shear 1970; Buskirk 1981). Based on the spatial organization and level of social behavior of the spiders, Burgess and Uetz (1982), defined three basic categories of sociality: "social" (or "cooperative", Riechert 1985), "colonial" and "territorial". In the text, I will use the term "cooperative" instead of the "social" category mentioned above, to avoid confusion when referring to social species (that is, species exhibiting any type of social structure).

Cooperative species live together in complex web-nests, cooperate in web construction and prey capture, and engage in communal feeding and sometimes indiscriminate brood care (adults taking care of offspring that are not necessarily their own). The majority of the social species produce cob or scaffold-line webs and belong to the spider family Theridiidae. The other prominent web type is the sheet web produced by several spider families. Included among the cooperative species are a few

representative from the non web-building vagrant and ambush spider categories (i.e., the genus *Diaea*, Thomisidae and *Tapinillus*, Oxyopidae).

Colonial spiders join individual webs together within a communal framework, but individuals build, occupy and defend their own webs within a colony. Orb-weaving spiders from the families, Araneidae, Tetragnathidae and Uloboridae are the only species with this type of social system. I describe this type of social system in more detail in the next section.

Finally, territorial species constitute the vast majority of spider species. These species are solitary with an overdispersion pattern of web distribution in preferred habitat. Non web-builders exhibit a similar pattern of dispersion in the placement of their retreats. Territorial behavior is energy-based with territory size determined by local prey availability (Riechert 1976, Riechert, 1982). The territories maintained by these spiders ensure individuals the prey levels required for survival and reproduction.

COLONIAL SPIDER SYSTEMS

Colonial spiders are basically territorial spiders that show increased tolerance towards nearest neighbors. The capture web here is the territory. Orb weavers are the prominent representatives of the colonial social structure in spiders. Numerous authors attributed the absence of cooperative behavior among the colonial orb-weaver spiders to the constraint imposed by the orb web. The architecture of the orb web, its physical properties and the precision required to build it seems to prevent colonial species from achieving cooperative social status (Buskirk 1975b, a; Rypstra 1979). On the one hand, orb webs are not cost effective to share. They cannot be built communally. Thus the individual building the web is put at considerable energetic cost relative to others that might take advantage of it. The architecture of the orb-web is also such that all the vibrations are transported to a particular place in it, the hub, the place at which all radii converge. Non-geometric webs (i.e., scaffold and sheet webs) may be better suited for cooperative behavior because vibrational cues are damped by these webs and information is not directed to a focal individual situated at some central location (Krafft 1979).

The existence of a defended territory limits the extent and types of interactions among members of the colony because direct contact is diminished as colony members are not generally allowed access to an individual's web. Typically, social activities in colonial spiders are restricted to the construction and maintenance of the common framework on which all of the orbs are built. However, in a few species (*Philoponella republicana*, Uloboridae; *Metabus gravidus*, Tetragnathidae; and *Parawixia bistriata;* Araneidae) individuals also share a common silken retreat (Buskirk 1975b, a; Fowler & Diehl 1978; Smith 1983; Sandoval 1987).

Agonistic encounters over webs would be expected to limit social interactions involving prey capture and feeding in this group. Reports of prey stealing or monopolization in spider colonies suggests the existence of conflicts involved in group foraging activities (Hodge & Uetz 1995). For instance, prey monopolization was reported in two species of *Philoponella* (*P. republicana*, Binford & Rypstra 1992; *P. raffrayi*, Masumoto 1998) after pairs of individuals captured prey.

Uetz & Hieber (1997) argue that *Philoponella* species and other uloborids might exhibit greater levels of sociality than other orb weaving groups because of the absence of poison glands in species within this family. Without venom, it is difficult for a solitary individual to subdue larger prey items. Thus group capture would be advantageous to individuals in uloborid colonies.

VARIATION WITHIN SPECIES

Colonial species, like cooperative ones, are mainly found in wet tropical regions, although some species are also present in semi-arid or temperate areas (e.g., *Cyrtophora*, *Metepeira* spp. and *Parawixia bistriata*: Araneidae, Uetz & Hieber 1997; *Philoponella*: Uloboridae, Smith 1982). In comparison to tropical and mesic habitats, in temperate and semi-arid habitats conditions are harsher, more seasonal and can be unpredictable. These differences in both abiotic (temperature, rainfall) and biotic (e.g., prey levels) conditions are thought to have an effect on life cycles and behavior. Uetz and co-workers, studying related colonial species of the genus *Metepeira* (Araneidae) found geographic variation in traits such as group size, spacing, life history, and reproductive output (Uetz & Hieber

1997). For example, *Metepeira atascadero* is found in habitats where conditions are typically severe and fluctuating. This species is solitary or lives in small groups. It reproduces only once a year and aggressively defends its capture web from conspecifics. *Metepeira incrassata*, on the other hand, lives in habitats that are primarily moist and more stable. This species forms groups ranging in size from tens to several thousands of individuals. It reproduces continuously, and exhibits overlapping generations. Although agonistic encounters are frequent in *M. incrassata* colonies, they are resolved with little aggression (Uetz and Hodge, 1990; Hodge and Uetz, 1995).

Another colonial species that is expected to exhibit geographic variation in life history and behavioral traits is *Parawixia bistriata*, which occupies a continuum of wet-dry sites. Prior to this study, *P. bistriata*'s populations has been studied in the Cerrado habitat of Brazil, a tropical savanna-dry forest (Fowler & Diehl 1978, Sandoval 1987, Fowler & Gobbi 1988, de Carvalho jr. 1997). I provide a brief review of what is known of the biology of this spider in the following section.

Parawixia bistriata AS A STUDY SYSTEM

Parawixia bistriata is a widespread species belonging to a genus of Neotropical, nocturnal orb weavers of the family Araneidae. Most of the species belonging to this genus are found in the Amazon rain forest area as well as in Central America and Eastern Brazil. *Parawixia bistriata* is unusual in terms of its distribution because, as opposed to other species in the genus, it is typically found in dry forests of southeastern South America. However, it also occurs in other habitat types ranging from wet forests to semi-arid areas (Levi 1992; F. Fernández Campón pers. obs.). There are also museum specimens collected in locations as far south as 30° S along the Paraná River, Argentina (Levi 1992). The margins of the Paraná and Uruguay rivers are extensions of tropical and subtropical forests into the temperate region termed the Atlantic forest. This may explain the presence of the spider at such high latitudes.

P. bistriata's social system is characterized by a gregarious stage during juvenile development and a solitary stage following maturation. Mating may occur either before or after dispersal from the colony (Fernández Campón, pers. obs.). The solitary female

dies before the egg sac she has laid hatches and the emerging spiderlings form a new colony at the site chosen by her. Immature instars share a communal retreat during the day, and each night individuals construct their own capture webs within a communal generated scaffold of silk lines that radiate out from the retreat to nearby vegetation. The retreat has very little silk but threads become thicker and more conspicuous as spiders grow. Retreats are three-dimensional and have an spherical shape. Newly hatched individuals build a retreat that measure between 5 to 15 cm of diameter and can reach 60 cm in diameter in some large colonies when individuals are in their subadult and adult stages. Spiders in the retreat are in very close contact forming a "ball". As dusk approaches, spiders leave the retreat to begin construction of their capture webs. At dawn they eat the secondary support lines and individual orbs before returning to the diurnal retreat. Only the principal threads are left to aid in the construction of orb-space webs the following evening. These threads may extend 30m or more from the diurnal retreat (Figs. 2 & 3).

Within a colony, juveniles molt nearly synchronously, within a few days of one another (Fowler & Gobbi 1988). Thus colonies are comprised of siblings of approximately the same age. There is some variation between colonies in the ages of cohorts at any given time (Fowler & Diehl 1978). Adjacent colonies may fuse with no overt aggression, forming 'supercolonies" (Sandoval 1987).

P. bistriata is the only described colonial species in the genus and the presence of a communal retreat differentiates *P. bistriata* from most other colonial spiders, as it represents the existence of higher levels of tolerance among conspecifics. When in the diurnal retreat, individuals show high conspecific tolerance as they huddle together in physical contact (Fig. 4).

Another characteristic exclusive to *P. bistriata* compared to other colonial species is the expression of facultative group capture and feeding, which appears to be cued by prey size. Individuals capture prey solitarily when the prey item is smaller than the spider and individuals participate in group capture and foraging when prey items are larger (Fig. 5). In some occasions when feeding in a group individuals seem to struggle to divide the prey item and sometimes succeed take a piece and feeding on it solitarily (F. Fernández

Campón, per. obs.; Fig. 6). Studies on other cooperative and colonial species indicate that capture success of large prey by an individual spider is lower than that of 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). Therefore by participating in group foraging *P. bistriata* might be able to exploit resources not available to solitary individuals. This can be an important trait that might have helped this species to successfully occupy habitats with low resources.

In the following parts of the thesis, I analyze different aspects of the life history and social behavior of *Parawixia bistriata* as they vary with habitat. In Part II I examine if there are geographic differences in life history characteristics of *P. bistriata*. In particular, I describe its life cycle and juvenile development and then I estimate the success of populations in habitats with different resource levels. Later, in Part III, I analyze the existence of behavioral differences in group foraging in populations found under different habitats and in Part IV I look for genetic or environmental causes of the behavioral differences. With this study I hope to understand what are the factors that could have caused or facilitated the evolution of social behavior in *P. bistriata* and whether its ability to utilize large prey could explain the distribution of the species under regions with different resource levels.

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Appendix

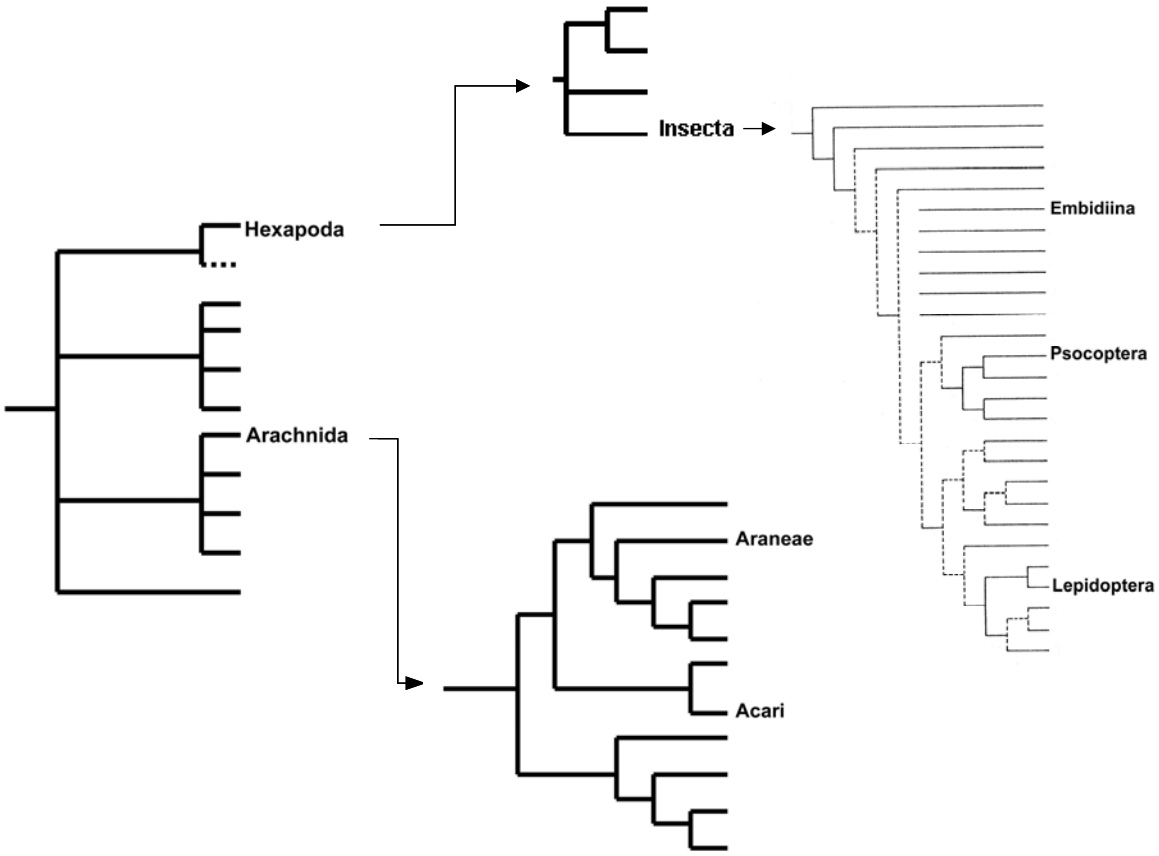


Figure A1. Phylogenetic representation of insect and arachnid orders with social species that exhibit convergent use of silk. Insect phylogeny modified from Kristensen 1981; arachnid phylogeny modified from Schultz 1990.



Figure A2. Colony of *P. bistriata* comprised of 6th instar individuals. The circle is enclosing the diurnal retreat and the arrow at the bottom left corner points to one of the main threads that serve as a frame of the orb webs built by spiders every night.

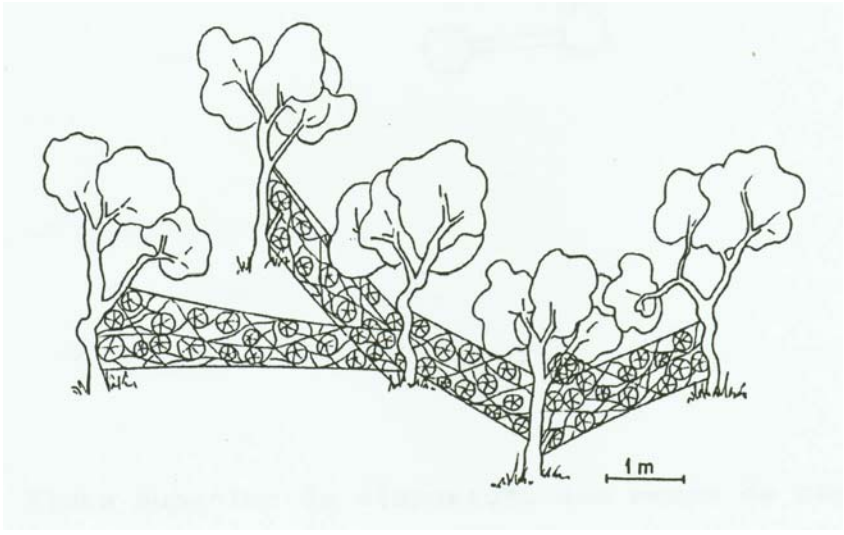


Figure A3. Schematic representation of the distribution of capture webs of *P. bistriata*. The vertical sheet of webs extends across open spaces. Drawing taken from Sandoval 1987.

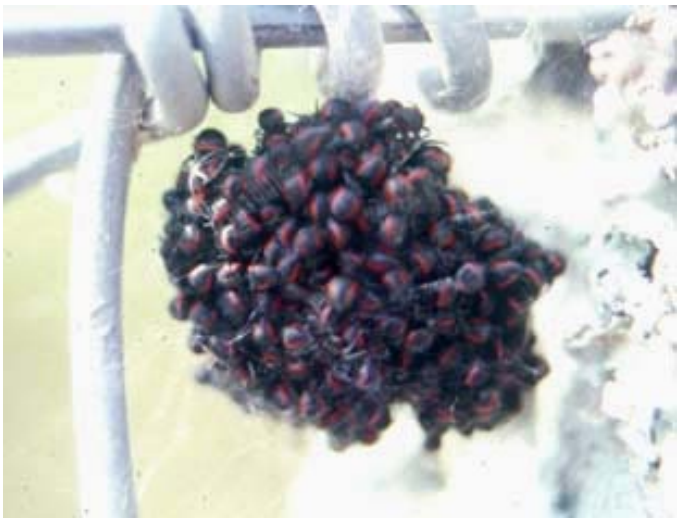


Figure A4. Colony of *P. bistriata* comprised by third instar individuals showing the way spiders huddled in the retreat during the day.

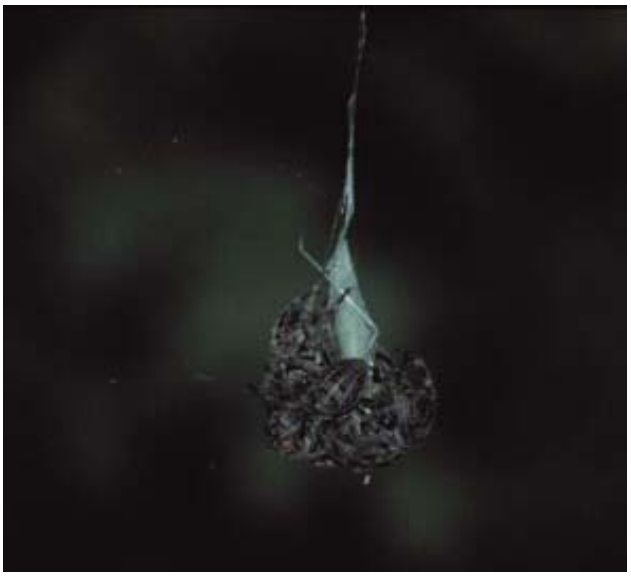


Figure A5. A group of sixth instar individuals of *P. bistriata* feeding on an Orthopteran.



Figure A6. An individual pulling a piece of the prey item on which a group of spiders were feeding.

Part II.

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

ABSTRACT

Patterns of juvenile development may be both influenced by and reflect adaptation to environmental conditions. The relationship between environment and pattern of juvenile development was examined in populations of a South American colonial orb-weaving spider, *Parawixia bistriata*, which in different parts of its range occupies sites that offer very different moisture regimes. Colonies from wet vs. dry habitats in the Chaco region of Argentina exhibit different phenologies. Results of reciprocal transplants of individuals completed between these habitat types suggest that observed variation in phenology may reflect plasticity in the inter-molt interval. Despite differences in resources and associated levels of constraint placed on spider development in dry vs. wet sites, there were no significant differences observed between native colonies occupying both habitat types in the number of eggs produced per clutch. Colony size was larger in the dry sites. However, transplants from wet to dry sites were negatively affected by the lower prey availabilities offered by dry sites: these transplanted individuals exhibited significantly lower growth rates and smaller clutches and they ultimately failed in reproduction. This suggests that traits other than the life history parameters I examined underlie population success in respective dry and wet Chaco habitats. Differences in foraging behavior or resource allocation patterns are likely targets for future study.

INTRODUCTION

Widespread species are likely to experience a diversity of environmental conditions and to exhibit differences in life history traits in response to this environmental variation. The sources of variation in life history traits within a species can be genetic or environmentally induced. One can compare reaction norms (the set of phenotypes expressed by a genotype across environments) for implicated traits to distinguish between these two factors (Stearns & Koella 1986; Carroll & Corneli 1999). The reciprocal transplant study makes it possible to examine reaction norms for traits that might show population divergence. If transplanted individuals exhibit the same phenotype as native individuals in both habitats, differences between populations are due to environmental effects. If differences between native and transplanted individuals exist in at least one of the habitats, genetic divergence underlies differences in the phenotypes with populations having different norms of reaction.

Higgins and Rankin (1996) argue that the fitness of an organism with a complex life cycle, such as an insect or a spider, is strongly influenced by traits that are associated with the individual's development such as inter-molt interval, the number of molts and the size increment associated with ecdysis (molting event). The number of molts and the inter-molt interval determine the age at maturity. The change in size at ecdysis and the number of molts determine the size at which an individual matures. Since such traits as the number of molts, the inter-molt interval and the size at ecdysis affect the timing of reproduction and the number of offspring produced, they may respond to environmental variation and thus be subject to change as a result of selection pressure.

In this study I examine potential life history trait variation in a widely distributed South American spider, *Parawixia bistriata* (Araneae, Araneidae) that is found in habitats with different seasonal constraints. In spiders, there is a close correspondence between foraging rate, growth, and fecundity. This makes them a good model for the study of the effect of the environmental conditions on development and reproduction. Moreover, the foraging rate of a spider is not only determined by the rate of encounter with prey but also by body temperature, which is itself a function of the physical environment (Riechert & Tracy 1975). Thus, differences in the biotic and abiotic

environment that affect foraging are reflected in the development and reproduction of individuals.

The effect of variability in food resources on the development of spiders has been shown in manipulative studies. Spiders may respond to experimentally induced changes in prey levels by modifying the number of molts and maturing later but at a similar size as under natural conditions (Miyashita 1968; Higgins 1992, 1993; Mayntz et al. 2003), or alternatively, by maturing after the same number of molts but at a smaller size (Mayntz et al. 2003). Thus, species or even sexes within a species may exhibited different developmental responses to changes in resources.

This study entails population comparisons of the colonial *P. bistriata* in dry vs. wet habitats at the same latitude (26° S) in the Chaco region of Argentina (Fig. A1). Although both habitat types exhibit dry and wet seasons, the duration and strength of the dry season is less severe in the wet habitat type. Spider colonies in the dry site thus experience lower prey levels. I completed colony censuses and found that differences in colony phenology exist between wet and dry habitats. I then completed reciprocal transplants to examine the mechanisms underlying the observed differences in population responses to environmental variation.

METHODS

Parawixia bistriata

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

Though this univoltine spider is typically found in dry forests, it frequents a diverse range of habitats from semi-arid scrub to wet forests in southeastern South America (Levi 1992; Fig. A1). Sandoval (1987) has studied the life cycle of *P. bistriata* in the Brazilian Cerrado, a mosaic of dry forest and savanna extending between 6° to 23° latitude (Fig. A1). She reported that adults are found in the fall, lay egg sacs at that time and die soon after oviposition. While the spiderlings actually hatch during the winter, they remain in

the egg case until spring when each clutch forms a new colony consisting of 2nd instar sibs (the spiderlings undergo one molt within the egg) and have a second molt soon after emergence from the sac. Individuals within a colony molt within a few days of one another (Fowler & Gobbi 1988) and the cohort remains aggregated in the colony until completion of the seventh molt when individuals mature. At this time, females leave the nest to initiate egg laying in isolation. Based on this phenology, the life cycle of *P. bistriata* is classified as stenochronous with reproduction on the fall (Schaefer 1987).

Study sites

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; Fig. 1). 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. There are corresponding differences in the species composition of the vegetation, in vegetation structure, and in insect abundances.

I established a pair of sites in eastern Wet Chaco (termed 'wet sites') and another pair of sites 400 km to the west in a transition area between Wet and Semiarid Chaco (termed 'dry sites'). The two wet sites were situated 80 km apart in the Formosa province of Argentina, Wet 1 at a provincial reserve, Guaycolec (26° 10' S, 58° 12' W), 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 the 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 the town on public-owned land. (I found that due to human disturbance it was not possible to complete experimental manipulations at the site Dry 2. Thus, this site only provided data on the developmental pattern of spiders at native colonies).

I assumed that the *P. bistriata* located at each site represented a distinct population and, thus, considered the two replicates for each region as independent samples within the respective habitat type. I based this assumption on: 1) the noted low vagility of adult spiders (adults traveled distances of only 200-500 m when dispersing from the colony at

reproduction; J. Kochalka pers. comm.; Fernández Campón pers. obs.), 2) the patchy distribution of colonies, and 3) the large distance between study areas (especially in the case of the wet sites).

Climatograms describing the temperature and precipitation patterns of dry and wet sites are shown in Fig. A2. Both habitat types have a marked dry season in the winter and wet summers during which 80 to 90% of the annual precipitation occurs. While the daily mean temperature regime is similar between habitat types, freezing days are more frequent and annual precipitation lower in the dry sites (Table A1). The pattern of precipitation differs as well. The wet sites exhibit two peaks in precipitation, one during the late spring (October to November) and a second, stronger period during the fall (March to April; DiGiácomo 2001). There is only one peak in precipitation in the dry sites (December to January).

Vegetation in the wet sites is a macro-mosaic of deciduous and semi-deciduous forests on the uplands and palm forests in lower lands. These forest patches are interspersed with grasslands and marshes. The natural upland forest is dominated either by *Schinopsis quebracho-colorado* (Schlechtendal) F.A.Barkley & T. Mey (Red quebracho), *Schinopsis balansae* Engler (Willow leaf red quebracho), and other *Schinopsis* species commonly referred to as quebracho colorado (Anacardiaceae) or by *Aspidosperma quebracho-blanco* Schlechtendal (Quebracho blanco; Apocynaceae). *Copernicia alba* Morong ex Morong & Britton (Caranday palm; Palmae) dominates the forested wetlands. Shrubs are most abundant in sites grazed by cattle, as are cacti of the genus *Opuntia* (Prickly pears; Cabrera 1971; Cabrera & Willink 1973). Colonies of *P. bistriata* are mainly found at the borders of forest patches.

Deciduous and xerophyllic tree species adapted to the annual periodicity of dry and wet seasons dominate the forested areas of the dry sites. *Schinopsis lorentzii* (Griseb.) Engler (Quebracho santiagueño) and *A. quebracho-blanco*, are the native dominants and are accompanied by the understory trees like *Prosopis kuntzei* Harms ex Kuntze (Itín, Fabaceae), *Cercidium praecox* (Ruiz & Pavon) Burkart & Carter (Brea; Caesalpinieae) and *Ziziphus mistol* Griseb. (Mistol; Rhamnaceae). Other plants include the cacti *Opuntia quimilo* Schumann (Quimil) and *Cereus coryne* Salm-Dyct (Cardón), spiny and

conspicuous bromeliads and towards the east, the palm *Trithrinax biflabellata* Barb. Rodr. (Carandilla; Arecaceae; Cabrera 1971). Some non-native tree species such as *Melia azedarach* L. (Paraíso or chinaberry; Meliaceae) are also interspersed with the natives.

Prey availability

I used Malaise traps to quantify prey availabilities in wet and dry habitats and to examine whether colonies are associated with higher prey levels than generally available at each site. The traps (Bioquip model #2875AG) had the shape of a square tent with four central vanes to stop insect flight and a collection head located at the top of the tent at two meters from the ground. I collected the insect biomass data over three sampling periods for each site during the field season extending from October 2002 to January 2003. I moved on to a different study area after each sampling period and thus censused sites sequentially in the order Wet 1, Wet 2 and Dry 1 throughout the field season. Two pairs of traps were set up at each site in places with colonies and without colonies. Traps were paired by locating one of the traps 10 meters north of a trap located at a colony site. (Colonies were removed prior to trap placement.) The actual insect samples were collected between 19:30-7:00 hr coinciding with the activity period of this spider. No samples were collected on rainy nights thus the potential eight-night sampling period varied from two to eight days.

Insects collected in each trap for each trap night were tallied as to taxonomic order and body length. They were then preserved in individual vials with 70% ethanol and were taken back to the laboratory where dry weight estimates were made. At the laboratory, ethanol was removed from the samples using filter paper. Samples were left to air-dry at room temperature for 24 hrs. They were then placed in a drying oven for 20 hrs at 66 ° C. The dried samples were weighed to 0.001 g using a Mettler electronic balance.

Transplants

I performed reciprocal transplants of spiders between habitats to identify the sources (genetic or environmental) of the differences in life history traits between populations from dry and wet habitats. No transplants were made within the immediate vicinity of

existing colonies (minimum distance to native colony was 200 m). 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 transplant colony was prepared for the move by cutting the segment of the branch where the retreat was located and placing it in a 1-liter plastic bottle that had been cut into two sections. The two sections were taped together for the move. Only the half holding the retreat was ultimately attached to a branch at the new site. (With the exception of two transplants, the spiders abandoned the retreat inside the bottle and built a new one nearby.) The transplanted retreats were placed on a branch close to the trunk of a tree and at a height between 1.5 to 2 m corresponding to the position observed in colonies comprised of individuals in their 3rd and 4th instars in the field (F. Fernández Campón pers. obs.; Sandoval 1987).

The ten 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 in their 3rd - 4th instar (15 June 2002). Five colonies were successfully established after having over-wintered in the dry site for a period of four months. The transplant of dry colonies to wet sites was completed on November 8, 2002 using colonies collected at the 3rd and 4th instar from a site located in the vicinity of Dry 1. (An earlier transplant in June failed as the two remaining colonies in Wet 1 could not be reached for censusing and only one super-colony of > 1,000 individuals was found in Wet 2.) Of the 10 colonies transplanted at the two wet sites, three colonies were successfully relocated at Wet 1 and five colonies at Wet 2.

Phenology and developmental traits

Spider development in native colonies was assessed over two field seasons from October to January in 2001-2002 and 2002-2003 and, in the case of transplanted colonies, during the second season from October to January 2002-2003. These periods correspond to mid spring to late summer in the Southern Hemisphere, which is the rainy season in the Chaco. Colonies were censused every 30 to 40 days and colony developmental stage (instar) was classified as that of individuals of the latest instar. Most of the colonies

within a site were of one or two consecutive instars. Because individuals within a colony molt in synchrony (Fowler & Gobbi 1988) individuals of the earlier instar would molt within a few days of the time of censusing.

The number of instars has been described by Sandoval (1987) and were later established in laboratory rearing. Instars are easily recognized by the color pattern in the field. I collected and dissected a number of colonies from the two habitats to examine the instar composition of individuals within the colony (N_{dry}=7, N_{wet}= 16). This permitted me to validate the method I used to classify colony developmental stage. All individuals in each of the sampling colonies were counted, sexed and weighed.

During each field census, I collected between 5 and 10 individuals from each colony to estimate growth rate and change in size at ecdysis. I weighed each spider using a field scale (Acculab model #PP-2060D) and measured its cephalothorax width using digital calipers. Because the cephalothorax is a hard part of the exoskeleton, it is a good indicator of an individual's growth during each molt. Spider mass is more indicative of foraging success within each instar and was used as an estimate of growth rate for comparisons among treatment groups. All individuals were returned to their respective colonies following measurement. I only utilized juveniles and subadult and adult females in the analysis of growth rate as Sandoval (1987) showed that sexes exhibit different pattern of growth. I used data on 5^{th} and 6^{th} instar individuals for the comparison of cephalothorax width of native and transplanted individuals from dry and wet habitats because these were the developmental stages present in the four treatment groups.

Clutch size

I use clutch size, the number of eggs produced per egg sac, as my estimate of female fitness. With one exception noted in the field (one female producing three egg sacs), females have been observed to produce one egg sac and die soon after that (M.C. de Carvalho Jr., pers. obs.; F. Fernández Campón pers. obs.; C. Sandoval pers. obs.) thus clutch size can be equated with female lifetime fecundity and used as a component of fitness. Egg sacs produced by native and transplanted individuals were collected in the field and maintained in the laboratory in the city of Formosa until hatching. Counts were

made of spiderling numbers at hatch along with the number of unhatched eggs to produce the total number of eggs per sac. Spiderlings were later returned to their site of origin. All the egg sacs produced by females from transplanted colonies that were found in the field were collected. I am confident of the correct identification of collected egg sacs produced by transplanted vs. native individuals. I discriminated between these on the basis of proximity to existing colonies and the appearance of the casing of the egg sacs: the outer silk layer of the sacs produced by females originating in wet sites is yellow, that from dry is white.

Colony size

Colony size was estimated by counting the number of individuals on the webs and the retreat during the nocturnal activity period. This is a non-destructive and effective way of censusing colonies as this species is active at night and most of the individuals of a colony are outside the retreat on their capture webs during the nocturnal foraging period. Only colonies with 6^{th} instar individuals were sampled. Colony size was estimated by two observers in the case of one census of seven colonies at Wet 1. A Spearman correlation was used to assess the degree of inter-observer reliability in colony size estimation: ($r_S = 0.93$, $N = 7$, $P < 0.05$). Subsequent estimations of colony size were performed by one or the other of these two observers.

Data analysis

I used a repeated measures ANOVA to test for habitat and temporal differences in insect availability between habitats. The independent variables between subjects (traps) were habitat type (wet or dry) and location within habitat (colony or non colony location). The variable time (corresponding to the three sampling periods) was the within subject variable. The dependent variable was insect biomass per trap night.

Data on the phenologies of native individuals from dry and wet sites consisted of small integer counts which violated the assumptions of parametric statistical tests. I applied a generalized linear model with Poisson errors, a log link function and type III significance tests (Poisson regression) to these data using the PROC GENMOD of SAS

version 8 (Stokes et al. 2000). Examination of the diagnostics (i.e., deviance and df) indicated that the data were under-dispersed. The data were thus scaled using the deviance to improve the fit to the model (Stokes et al. 2000). In this case, the type III analysis is based on the F probability distribution instead of χ^2 distribution. I selected the model that presented the best fit to the data using a likelihood-based χ^2 test (Stokes et al. 2000). Variables or interaction terms that were not significant were excluded from the model. In the Poisson regression model the variables habitat (wet vs. dry), year (field season 1 vs. 2) and day (continuous variable that identifies the day within a field season) were the explanatory variables. The developmental stage of a colony (instar) was the response variable. To assign values to the variable day, the first day of the study period (10/15/2001) was assigned the number 1 and subsequent days were numbered up to 118. (Note that in the graphical representation of these results, monthly averages are shown for ease of interpretation).

I performed a generalized linear model similar to the one described above for the comparative analysis of the phenologies of native vs. transplanted individuals. In this new model, I included the variables origin (habitat of origin), rearing environment (habitat type where colonies had developed) and day (defined as in the previous model) as explanatory variables. Again, the developmental stage of a colony was the response variable. I used the Bonferroni correction by dividing α (0.05) by the number of multiple comparisons performed when performing multiple comparisons to determine which groups were causing the significant interaction effects in the analysis, (Sokal & Rohlf 1995).

I used the increase in spider mass per unit time as my estimate of growth rate. The variable spider mass was log transformed to linearize its relationship with the variable days. I applied a generalized linear mixed model (GLMM) to the growth rate data. Data on individuals of wet and dry origin were analyzed separately. The GLMM included the variables day and habitat (native or foreign) and the interaction day x habitat as fixed factors and site nested within habitat as a random factor. I considered site as a random factor because there were several possible sites within each habitat type (rearing environment) that could be used in this study (as opposed to only two types of habitats). I

was interested in answering the question of whether habitat type had an effect on the life cycle (and growth rate) of individuals and not the specific question of whether it differed among the specific sites used. Thus it was more appropriate to include "site" as a random effect. A GLMM was also used when I analyzed the differences in the change of size at ecdysis (cephalothorax width) between native and transplanted individuals of both dry and wet habitat of origin. The model included the variables origin, rearing environment and instar as the fixed factors and site nested within rearing environment as the random factor.

Clutch size and the size of native colony data did not meet normality assumptions, thus, I used the rank of these data as dependent variables in analyses of individual and colony success. The GLMM for clutch size included the variable site nested within rearing environment as a random factor. Fixed factors in this model were the presence or absence of egg sac parasitoids, rearing environment and habitat of origin of spiders (as described above). The size of native colonies was also analyzed using a GLMM, with habitat as the independent variable and site nested within habitat as a random factor.

RESULTS

Prey availability

The repeated measures ANOVA indicated a significant effect of habitat ($F_{1,6} = 16.29$, $P < 0.01$) but no effect of trap location within site on prey availability ($F_{1,6} = 0.05$, NS; Table A2). Prey abundance as measured by biomass was higher in the wet sites than in the dry site (mean ± S.E [g].: $Dry_1 = 0.16 \pm 0.02$; $Wet_{1+2} = 0.28 \pm 0.04$; Table A3).

Phenologies

Sample colonies in both habitat types were comprised primarily of two instars: 57% of one instar and 41% of the previous instar. Classifying the developmental stage of a colony by the latest of the instars in this study is well supported by these results. In the colonies comprised of individuals of three different instars, individuals of the earliest instar constituted only between 2% to 4% of the colony. The proportion of colonies

containing individuals of three different instars was larger in the dry sites (0.71) than in the wet sites (0.19; $\chi^2 = 5.96$, df = 1, $P < 0.02$).

Native colonies. Results of the generalized linear model analysis of colony stage of development showed significant temporal variation within years (significant effect of the variable day), significant year and habitat effects as well as a significant interaction among all three variables (Table A4). The interaction effect between year and habitat was not significant and was excluded from the final model. Absence of such an interaction indicates that consistent differences in the developmental stage of colonies from dry and wet habitats occurred during the two years in addition to the differences found between years within a habitat (significant effect of the variable year). Overall, a two-instar difference is exhibited in colony development between the wet sites (more advanced phenology) and the dry sites (Fig. A3). The significant three-way interaction effect reflects the differences in the developmental rates (change in the developmental stage in time) observed between colonies in the two habitat types sampled during the two years.

Native and transplanted colonies. The generalized linear model analysis of the stage of colony development for native vs. transplanted colonies indicates that there was significant temporal variation within year (day), as well as significant effects of the habitat of origin and rearing environment (Table A5). There were also two significant interaction effects: between rearing environment and origin and between origin and day. These relationships are shown in Fig. A3. The significant rearing environment effect reflects the fact that colonies at wet sites are composed on average of later instars over the course of the season. Likewise native and transplanted colonies of wet origin are developmentally more advanced than natives and transplants of dry habitat origin.

The significant interaction between rearing environment and origin indicates that the two classes of transplants exhibited different developmental responses. I completed contrasts to further delineate these differences (Table A6). While the developmental stage of transplants of wet origin differed from that of native wet site colonies, similar differences were not observed for colonies of dry origin. The significant contrast effect

reflects the fact that transplants of wet origin showed delayed development compared to the native colonies from wet sites (Fig. A3).

Developmental traits

The growth rates (change in mass with time) of native and transplanted individuals of dry origin (represented in the model by the interaction habitat x day) were not significantly different from one another (Table A7; Fig. A4). However, the growth rate of native individuals from wet sites was higher than the growth rate of individuals of wet origin transplanted to the dry sites (Table A7; Fig. A4). Differences in the average mass of spiders during the time following transplantation and the beginning of data collection were reflected in the significant effect of rearing environment in this analysis.

Cephalothorax width (CW) differed between instars and between individuals of dry and wet habitat origin (Fig. A5; Table A8). However, rearing environment was not a significant effect in the model, implying that CW is not a plastic trait. Multiple comparisons indicated that differences in CW among individuals from dry and wet origin occurred among 5^{th} instar individuals ($t = 3.94$, $df = 223$, $P_{adj} < 0.01$) but not among 6^{th} instar individuals ($t = -0.55$, $df = 224$, $P_{adj} = 0.95$).

Clutch size

Some of the egg sacs collected in the field had been parasitized (Table A9). The number of unhatched eggs and spiderlings in parasitized egg sacs could be counted in all egg sacs except for two sacs produced by individuals of wet habitat origin transplanted to the dry site. In these sacs, the egg mass was sufficiently decomposed such that individual eggs could not be counted. The presence of parasitoids did not affect number of eggs produced per sac ($F_{1,57} = 2.15$, $P = 0.15$). Although a significant three-way interaction effect was noted (Table A10), multiple comparison analysis indicated that the only significant difference in the number of eggs was between parasitized sacs produced by individuals transplanted to wet habitat (DW) and the non-parasitized sacs produced by individuals transplanted to dry habitat (WD) (DW vs. WD: $t = 3.27$, $df = 57$, $P_{adj} = 0.03$). Because no significant differences in the number of eggs per parasitized and

unparasitized sacs were observed within treatments groups, it was possible to pool parasitized and unparasitized egg sacs in the examination of the effect of the rearing environment and habitat of origin.

Clutch sizes of individuals reared in wet sites were significantly larger than noted in the dry habitat ($F_{1,57}$ = 7.01, P = 0.01; Fig. A6). There was also a habitat of origin effect but no significant interaction between rearing environment and habitat of origin. The significant effect of habitat of origin indicates that overall sacs produced by individuals originating in the dry habitat had more eggs than sacs produced by individuals of wet habitat of origin (Fig. A6, Table A10). Multiple comparison analysis indicated that clutch sizes produced by native individuals in both habitats did not differ (dry native vs. wet native: t = 1.06, df = 57, P_{adj} = 0.29). Conversely, within wet habitats the number of eggs in sacs produced by transplanted individuals was significantly larger than native individuals (transplant to wet vs. wet native: t = 2.86, df = 57, P_{adj} = 0.02) but was not different to those produced by native individuals in the dry habitat (dry native vs. transplant to wet: t = -2.28, df = 57, P_{adj} = 0.07). Statistical comparisons involving sacs produced by individuals from wet habitat transplanted to dry habitat were not possible due to the small sample size (N = 2). The number of eggs per sac in these two sacs was at the lower end of the spectrum noted for the other treatment groups. This fact is reflected in Fig. A6.

Colony size

The size of native colonies , as indicated by the number of individuals, differed between habitats ($F_{2,51}$ = 114.39, P < 0.01). Average colony size in the dry sites was twice the size of colonies in the wet sites (Table A11).

DISCUSSION

The phenologies of native individuals from dry and wet habitats differed in both years during the months this study was conducted. Comparison of the developmental pattern of native and transplanted individuals suggested that while some traits such as the inter-molt interval can be induced by environmental conditions, others such as the change

in size at ecdysis are fixed characters. Despite differences in resource levels, clutch sizes produced by native individuals of dry and wet habitats were similar. The absence of an effect of differences in resources was also indicated by the larger colony sizes in dry habitats. Transplanted individuals, however, seemed to be affected by the change in local conditions. While there were no significant differences in clutch sizes produced by native and transplanted individuals of dry habitat origin (dry natives and transplant to wet), individuals transplanted to the dry site produced a smaller number of eggs per sac than individuals in their original wet habitat.

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

The change in the developmental rate of individuals of wet habitat origin transplanted to the dry site suggests that differences in phenologies found in native populations are induced by environmental factors affecting the inter-molt interval. Native individuals in wet sites molted four times during the five months that elapsed between transplantation and the start of the data collection period when they were in the 7^{th} instar. On the other hand, individuals from colonies transplanted to the dry site were still in the 5^{th} instar and molted only twice during those five months (Fig. A3). Failure to find differences in the developmental rate of native and transplanted individuals of dry habitat

origin could be attributed to the short duration of time the transplanted individuals had been in the novel environment previously to being sampled rather than to the possibility that the inter-molt interval is a fixed character in individuals of dry habitat origin. In contrast, change in the size at ecdysis (measured as a change in cephalothorax width during molts) was found to be a fixed character. This suggests that individuals need to reach a certain size threshold before they can molt.

The existence of a threshold size for molting could be a constraint to maturation before the end of the growing season. Late maturing spiders would encounter two problems: 1) during the adult stage they would have difficulty reaching energy requirements for oviposition, or 2) there may not be surviving males (Henschel et al. 1995). This constraint can be particularly important for individuals under low resources and a more severe dry season if the number of molts is also a fixed character (Higgins & Rankin 1996). Conversely, if the number of molts is a plastic trait, individuals under low resources would mature before the growing season ends but after fewer molts and having achieved a smaller size. This incurs a cost of lower fecundity (Higgins & Rankin 1996; Higgins 2000). I did not find evidence of a decrease in fecundity in native individuals in the dry sites compared to native individuals in the wet sites. While clutch sizes of individuals of wet habitat origin transplanted to the dry site were smaller than in their native wet habitat, native individuals in the dry sites did not produce smaller clutch sizes. It is still possible, however, that a fixed size at ecdysis is constraining the life cycle of individuals in the dry habitat type and that not all individuals mature in time to reproduce before the end of the wet season. If that is the case, as judged by the clutch sizes and the size of colonies, individuals that get to reproduce in the dry sites seem to have been able to overcome constraints imposed by the seasonal patterning and their developmental pattern.

Alternatively, individuals in wet habitats can be under strong constraints imposed by environmental factors such as precipitation. High levels of precipitation may negate the benefits of higher levels of prey by the destruction of the capture webs as occurs in the social funnel-web spider *Agelena consociata* (Agelenidae) in Gabon (Riechert et al. 1986). Necessary rebuilding of webs consumes an important energy investment in silk.

During the rainy season in Gabon this puts small colonies at selective disadvantage as more silk investment per individual is required in small colonies. Results reported in this study on *P. bistriata* show that the growth rate and clutch sizes of both native and transplanted individuals found in the wet habitat are not negatively affected by conditions in this type of habitat such as precipitation. This suggests that precipitation levels are not a constraint to individuals in the wet sites.

Native populations from dry and wet habitats seem to have diverged in characters affecting their fecundity (clutch size). Although in wet habitats clutch sizes were larger regardless of the habitat of origin of females, a significant origin effect and the absence of an interaction between origin and rearing environment indicates that females of a dry vs. wet habitat of origin are affected differently by local conditions (different reaction norms).

Developmental traits do not seem to be causing the differences in fecundity of native individuals in dry and wet populations. None of the developmental traits examined in this study exhibited divergence between habitat type. There might be other traits (e.g., physiological, behavioral) that can explain the divergence in fecundity found. Differences between the dry and wet populations might be due to physiological differences: they might differ in the efficiency to allocate resources into the production of eggs (Hassall et al. 2005). Alternatively, there can be behavioral differences affecting their foraging success. Because *P. bistriata* exhibits facultative group prey capture and communal feeding, differences in the tendency to capture and share large prey between populations can affect the amount of food taken by colony members and how that food is distributed which in turn can effect their fecundity. Further examination of physiological and behavioral traits in *P. bistriata* would help understand adaptations this species might have to inhabit different environments.

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Appendix

Table A1. Temperature and precipitation between 1988-2000 for wet site 2 and a site adjacent to the dry sites.

		WET SITES	DRY SITES
Annual rainfall (mm)	Mean	1,500	827
	Max.	2,022	1,053
	Min.	909	533
Annual temperature (°C)	Mean	22	21
	Max.	27	27.1
	Min.	16	15
	Freezing days	unusual	Avg:13 (2-22)

Table A2. Repeated measures analysis of variance of insect dry biomass sampled per trap per night.

Factors	Source	Degrees of freedom		*F*	*P*
		Num.	Den.		
Between subject	Habitat	1	6	16.29	< 0.01
	Location	1	6	0.05	0.83
	Habitat x Location	1	6	0.01	0.92
Within subject	Time	2	12	0.47	0.63

Table A3. Insect dry biomass (g) sampled per trap per night in dry and wet sites.

Time*	Dry 1	Wet 1	Wet 2
1	0.19 ± 0.04	0.19 ± 0.01	0.35 ± 0.11
2	0.11 ± 0.02	0.36 ± 0.05	0.32 ± 0.05
3	0.17 ± 0.02	0.25 ± 0.05	0.16 ± 0.06
Average	0.16 ± 0.02	0.26 ± 0.03	0.30 ± 0.03

*the variable Time represents each of the sampling periods at each site.

Values are expressed as mean ± S.E. of biomass sampled by four traps used during each sampling period, except for the site Wet 2 during the third sampling period when only two traps were used (see text for explanation).

Table A4. Generalized linear model analysis of the developmental stage of native colonies in both habitats during the two field seasons (Poisson errors, log link).

Source	Degrees of freedom		F	$P > F$	χ^2	$P > \chi^2$
	Num.	Den.				
Day	1	114	142.64	< 0.01	142.64	< 0.01
Habitat	1	114	30.76	< 0.01	30.76	< 0.01
Year	1	114	16.22	< 0.01	16.22	< 0.01
Habitat x Year x Day	3	114	13.01	< 0.01	13.01	< 0.01

Deviance = 6.59; df = 114.

Table A5. Generalized linear model analysis of the developmental stage of native and transplanted colonies in both habitats (Poisson errors, log link).

Source	Degrees of freedom		F	$P > F$	χ^2	$P > \chi^2$
	Num.	Den.				
Day	1	65	124.11	< 0.01	124.11	< 0.01
Rearing environment	1	65	7.06	0.01	7.06	< 0.01
Origin	1	65	30.26	< 0.01	30.26	< 0.01
Rearing env. x Origin	1	65	6.08	< 0.02	6.08	< 0.02
Origin x Day	1	65	9.07	< 0.01	9.07	< 0.03

Deviance = 3.64; df = 65.

Table A6. Contrasts of parameters estimates for the interaction effect rearing environment X habitat of origin. The model was described in Table A5.

Contrasts	Degrees of freedom		F	$P > F$	χ^2	$P > \chi^2$	Adjusted P
	Num.	Den.					
WW vs. WD	1	65	13.41	< 0.01	13.41	< 0.01	S
WW vs. DW	1	65	48.24	< 0.01	48.24	< 0.01	S
WW vs. DD	1	65	34.93	< 0.01	34.93	< 0.01	S
WD vs. DW	1	65	19.52	< 0.01	19.52	< 0.01	S
WD vs. DD	1	65	15.25	< 0.01	15.25	< 0.01	S
DW vs. DD	1	65	0.02	0.89	0.02	0.89	NS

WW: wet native; WD: transplanted to dry habitat; DW: transplanted to wet habitat; DD: Dry native. Adjusted cut-off P value = 0.008.

Table A7. General linear mixed model of growth rate of individuals of dry and wet origin

Origin	Source	Degrees of freedom		*F*	*P*
		Num.	Den.		
Dry	Day	1	200.0	210.13	<0.01
	Rearing environment	1	61.60	2.28	0.14
	Day x Rearing env.	1	200.00	0.00	0.99
Wet	Day	1	231.00	556.47	<0.01
	Rearing environment	1	2.98	30.32	0.01
	Day x Rearing env.	1	231.00	9.21	< 0.01

Table A8. General linear mixed model of cephalothorax width of native and transplanted individuals of dry and wet origin.

Source	Degrees of freedom		*F*	*P*
	Numerator	Denominator		
Instar	1	182	141.21	< 0.01
Rearing environment	1	1.42	0.00	0.99
Origin	1	222	4.89	0.03
Rearing env. x Origin	1	222	0.62	0.43
Instar x Rearing env.	1	224	1.22	0.27
Instar x Origin	1	182	8.97	< 0.01
Rearing env. x Origin x Instar	1	224	0.55	0.46

Covariance parameter estimates: Site(Rearing environment) = 0.01; residual = 0.04

Table A9. Incidence of parasitism in egg sacs produced by native and transplanted individuals in dry and wet sites.

	Wet Native		Dry Native		Transplant to Wet		Transplant to Dry
Site	Wet 1	Wet 2	Dry 1	Dry 2	Wet 1	Wet 2	Dry 1
Parasitized	1	1	2	3	7	0	2
Sacs collected	6	15	12	14	10	5	2
% Parasitism	17	7	17	21	70	0	50

Table A10. Generalized linear mixed model analysis of clutch size of parasitized and non-parasitized sacs.

Source	Degrees of freedom Num.	Den.	*F*	*P*
Parasitized	1	57	2.15	0.15
Rearing environment	1	57	7.01	0.01
Origin	1	57	12.35	< 0.01
Rearing env. x Origin	1	57	0.46	0.50
Rearing env. x Origin x Parasitized	2	57	3.40	0.04

Covariance parameter estimates: Site(Rearing environment) = 0.00; residual = 282.03

Table A11. Size of native colonies found in the dry and wet sites

Site	Colony size (mean ± SE)	Colonies sampled
Dry 1	259.57 ± 57.57	8
Dry 2	278.50 ± 53.85	7
Wet 1	157.24 ± 33.24	21
Wet 2	89.41 ± 36.94	17

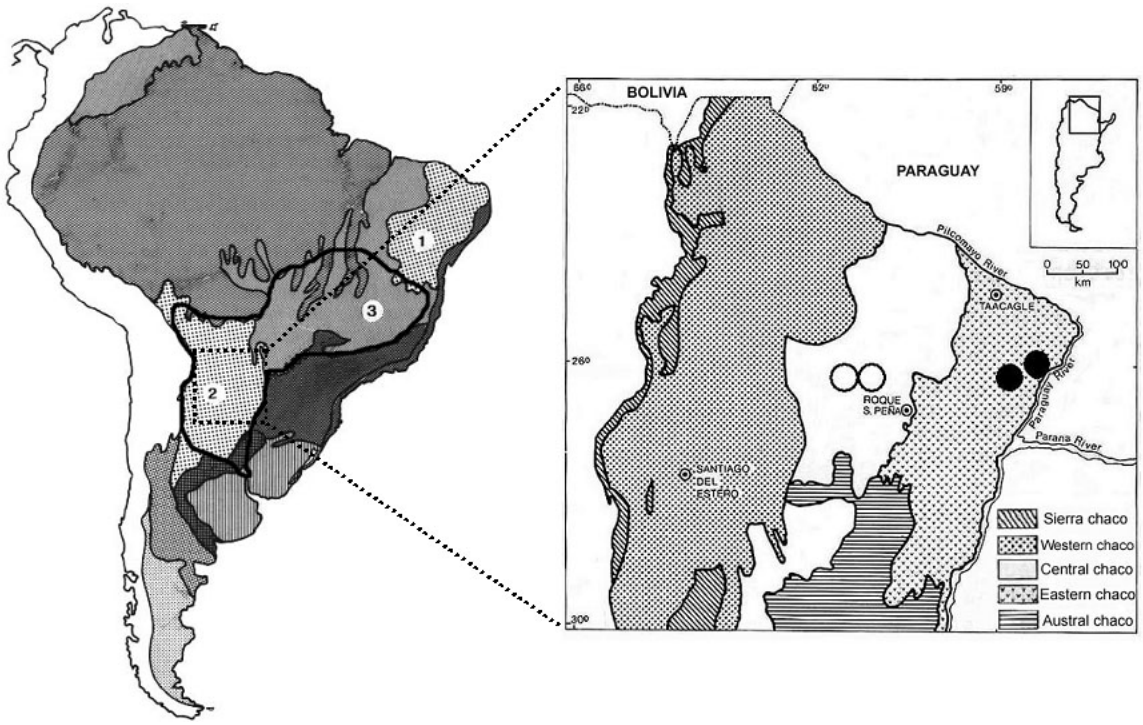
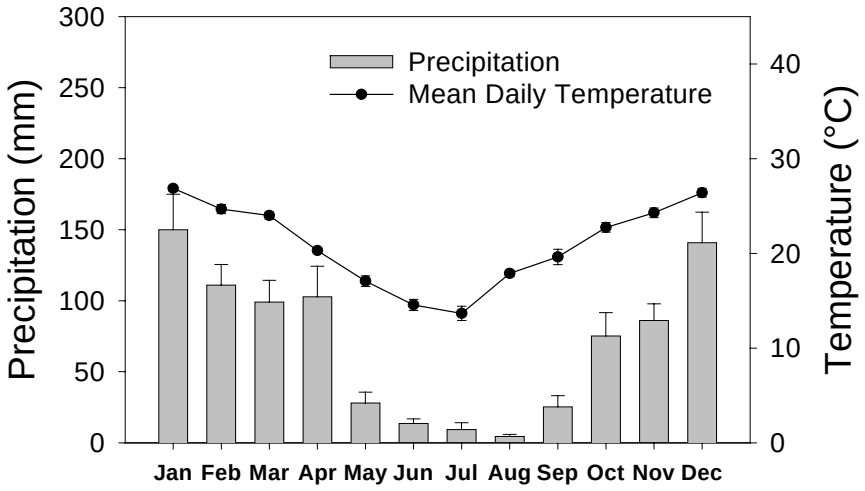


Figure A1. Geographic distribution of *P. bistriata* (black solid line). 1: Caatinga; 2: Chaco; 3: Cerrado. The enlarged insert to the right shows location of the study sites (dry sites: white circles; wet sites: black circles). Maps adapted from (Bucher 1982).

Figure A2. Climatograms for dry (A) and wet (B) sites during the period 1988 – 2000. Bars correspond to average monthly precipitation and the line represents average daily temperature per month. Wet site 2 data source: DiGiácomo 2001; dry sites data source: J. Pérez, unpublished data; collected in a site located 2 km north of the site Dry 1.

A.


Precipitation
Mean Daily Temperature
Precipitation (mm)
Temperature (°C)
300
250
200
150
100
50
0
40
30
20
10
0
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec

B.

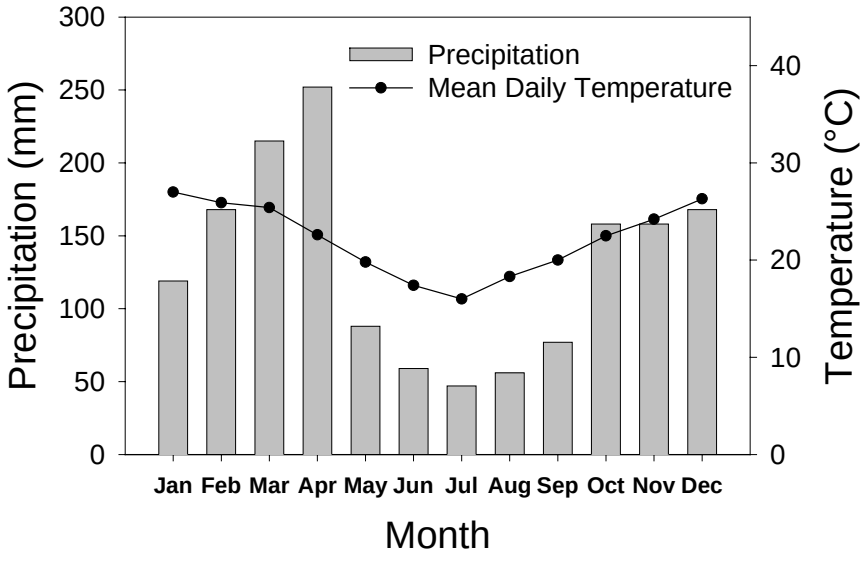
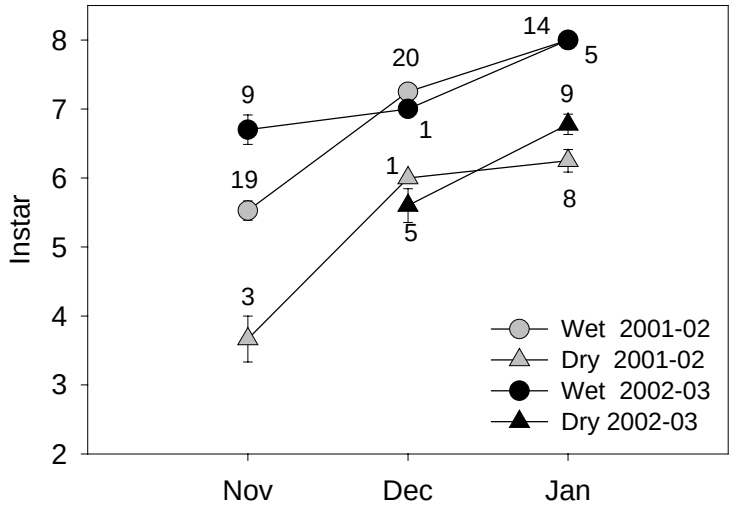

Precipitation
Mean Daily Temperature
Precipitation (mm)
Temperature (°C)
300
250
200
150
100
50
0
40
30
20
10
0
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
Month

Figure A3. Developmental pattern of native and transplanted colonies of *P. bistriata*. A) Developmental pattern of native colonies during the study period Nov'01-Jan'02 and Nov'02–Jan'03. B) Developmental pattern of native and transplanted colonies in wet and dry habitats during the season Nov'02-Jan'03. Numbers next to symbols are the number of colonies sampled during a month. Error bars indicate standard errors.

A.


Instar
8
7
6
5
4
3
2
Nov
Dec
Jan
14
5
20
9
9
1
19
1
8
5
3
Wet 2001-02
Dry 2001-02
Wet 2002-03
Dry 2002-03

B.

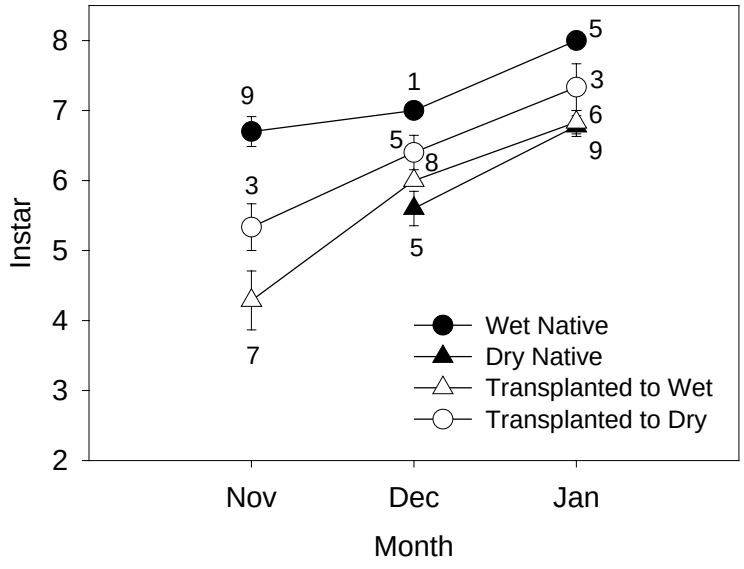
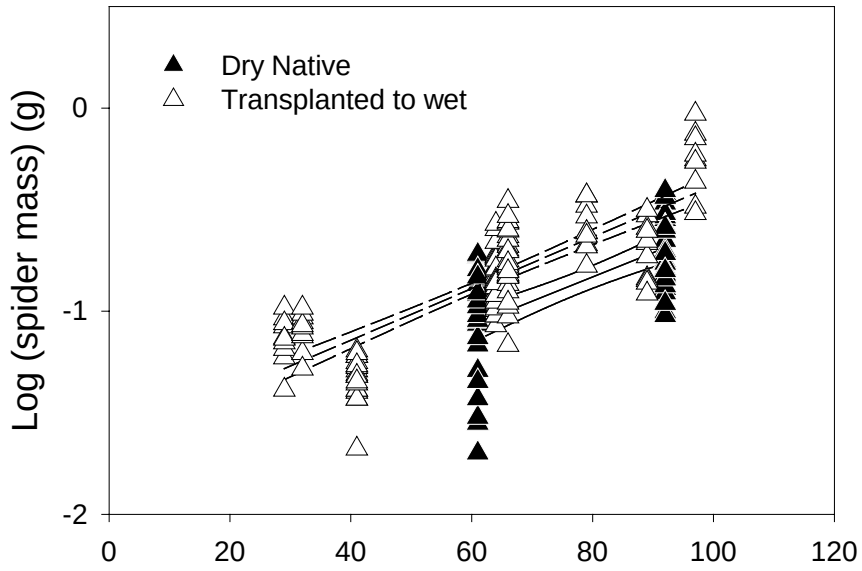

Instar
8
7
6
5
4
3
2
Nov
Dec
Jan
Month
5
1
3
9
6
5
8
9
3
5
7
Wet Native
Dry Native
Transplanted to Wet
Transplanted to Dry

Figure A4. Growth rate of populations originally from dry (A) and wet (B) habitats. Growth rate was calculated as the change in mass of individual spiders as a function of time (days since beginning of the study season staring on Oct 15th). Solid lines are the estimated regression functions and 95% confidence intervals for native colonies; dash lines are regression functions and 95% confidence intervals for transplanted colonies.

A.


Dry Native
Transplanted to wet
Log (spider mass) (g)
0
-1
-2
0
20
40
60
80
100
120

B.

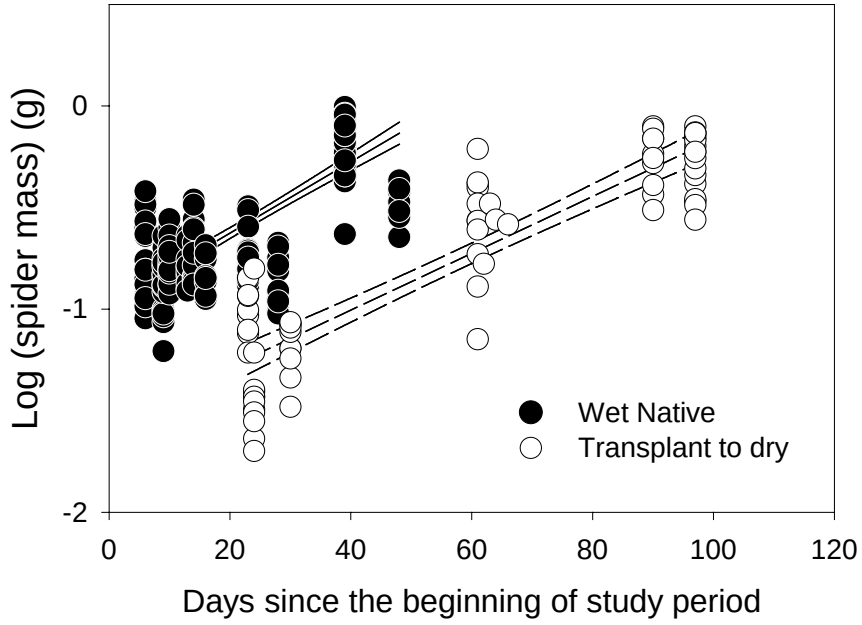
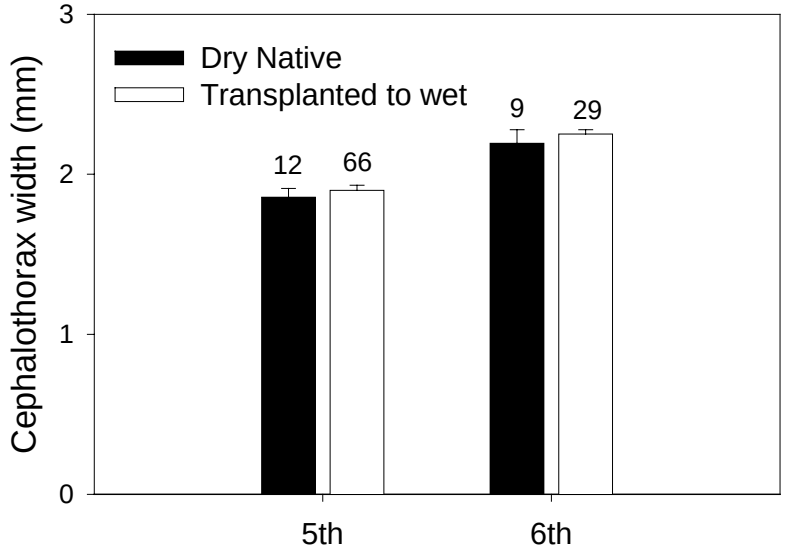
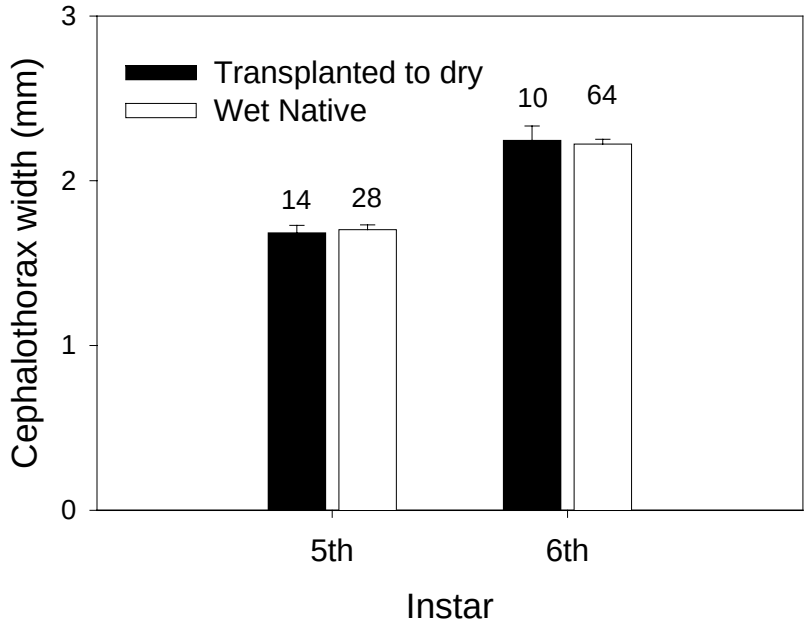

Log (spider mass) (g)
0
-1
-2
0
20
40
60
80
100
120
Wet Native
Transplant to dry
Days since the beginning of study period

Figure A5. Cephalothorax width by instar of individuals originally from dry (A) and wet habitat (B). Number above bars indicate sample sizes; error bars indicate standard errors.

A.


Dry Native
Transplanted to wet
Cephalothorax width (mm)
0
1
2
3
12
66
9
29
5th
6th

B.


Transplanted to dry
Wet Native
Cephalothorax width (mm)
0
1
2
3
14
28
10
64
5th
6th
Instar

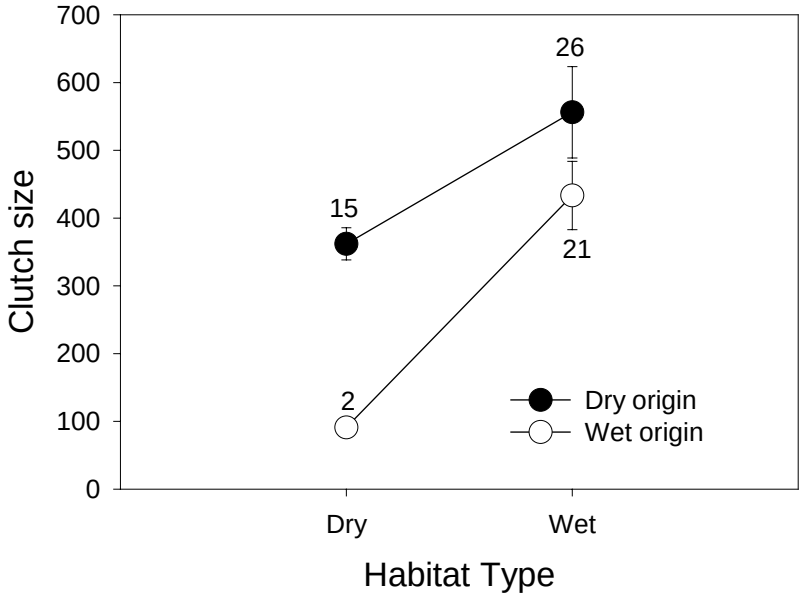


Figure A6. Clutch size (no. of eggs per sac) of native and transplanted individuals in both habitats. Numbers over circles indicate sample sizes; error bars indicate standard errors.

Part III.

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

ABSTRACT

In animal groups whose focus is on juvenile growth, prey attributes and individual access to prey can influence the level of sociality exhibited within local populations or species. Models examining the evolution of group foraging predict that if an individual is able to monopolize a prey item, it should not permit others to join in the capture of or feeding on that prey. If prey monopolization is not possible, individuals should allow others to join due to a high cost of prey defensibility. Hunger level can affect the above predictions through its effect on the perceived value of a prey item: an increase in the tendency to forage in groups is expected under higher hunger levels. I conducted a study on the foraging behavior 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 the frequencies 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 focal spider and others foraging in its vicinity. Individuals exhibited a higher tendency to capture prey and feed in a group as the size of the prey increased. In addition, spiders from dry habitats, which offer low prey levels, had a higher tendency to attack prey collectively than spiders from wet sites where prey levels were higher. Although there were no between-habitat differences in grouping tendency when feeding, sizes of feeding groups were larger at dry sites. Spider - spider competitive interactions during foraging were more frequent in groups from dry sites than those from wet sites. Thus, despite the higher aggression levels in interactions among individuals from dry sites, group foraging is more prevalent in these sites. This can increase the amount of food obtained by individuals in colonies at the dry sites.

INTRODUCTION

In social species, interactions among members of the group can have a differential 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 1999). In breeding societies, most social activities are associated with securing reproduction and the rearing and protection of offspring (e.g., social Hymenoptera, cooperatively breeding birds and mammals; Jennions & Macdonald 1994; Keller & Reeve 1994). Foraging societies, on the other hand, are primarily influenced by foraging constraints rather than reproductive ones, and most of the social behavior exhibited within these groups has an impact on individual growth (e.g., foraging, thermoregulation; Costa & Pierce 1997). These groups generally consist of juvenile individuals, each pursuing a goal of achieving a maximum rate of growth. 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 1999).

Some species of social spiders constitute foraging societies. In these groups, spiders can indirectly receive higher levels of food acquisition due to the deflection of insects from webs first encountered to neighboring webs ("ricochet effect", Uetz 1989). Spiders may also benefit directly from living in a colony by actively participating in the capture and or feeding on prey that encounter neighboring webs (Fowler & Gobbi 1988; Uetz 1988; Breitwisch 1989; Uetz 1992; Willey & Jackson 1993; Uetz 1996; Masumoto 1998; Whitehouse & Lubin 1999; Amir et al. 2000). The prey items caught in groups are usually larger prey than the items caught by individual spiders (Nentwig 1985; Ward & Enders 1985; Rypstra & Tirey 1991; Pasquet & Krafft 1992). Through group prey capture, individuals thus utilize a broader range of prey types that include larger prey items than a solitary individual could handle and this can have an important effect on individual growth.

There are at least two factors that can affect the occurrence of group foraging. First, the size of the prey can increase the likelihood of group capture. Packer & Ruttan (1988)

developed a series of models that incorporate payoffs to analyze the circumstances under which it is advantageous to hunt 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 hunt individually on this prey. Because large prey items are difficult to monopolize, the occurrence of group capture would 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 a spider's willingness to accept the risks and energy expenditure associated with prey capture (Riechert & Luczak 1982; Lubin & Henschel 1996; Ainsworth et al. 2002). Hungrier individuals could show a higher tendency to participate in group capture as hunger might increase the perceived value of a prey item. Higher hunger levels could lead to larger foraging groups and corresponding higher level of aggressive interactions as individuals within the group attempt to defend the resource against prey monopolization by other individuals

In this study, I examine prey capture behavior of *Parawixia bistriata,* a territorial group living spider species from the Chaco in Argentina. I compare the degree to which group foraging is related to food availability and evaluate the following predictions: (1) the strength of group response in the tendency to forage in a group and the number of individuals participating in those groups increases with increasing prey size and hunger stress; (2) interactions between the focal and neighboring spiders participating in group foraging is more frequent in colonies under low prey conditions.

METHODS

Study species

Parawixia bistriata (Araneidae) is a territorial group living spider. Individuals defend their capture webs from conspecifics but they forage in groups depending on the

size of the prey (Fowler & Gobbi 1988; de Carvalho Jr. 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.

Study sites

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 of and temporal variability in precipitation patterns 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 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.

The climate and vegetation structure in dry and wet sites is compared in Part II. Briefly, both habitat types offer a marked dry season in the winter and wet summers during which 80 to 90% of the annual precipitation occurs. While the daily mean temperature regime is similar between habitat types, freezing days are more frequent and annual precipitation lower in the dry sites. Insect availability in the two wet sites during a field season from October 2001 to January 2002 (measured as the insect dry biomass sampled by a Malaise trap per night) was almost twice the biomass sampled in the site Dry 1(mean ± S.E [g].: Dry = 0.16 ± 0.02; Wet = 0.28 ± 0.04). From these results and the fact that native and transplanted individuals' growth rate is lower in dry sites than in wet sites (Part II) I drew the conclusion that individuals in the dry sites are under stronger

hunger stress. Thus dry and wet habitat types represent high and low levels of hunger stress, respectively.

Data collection

Occurrence of group feeding under natural conditions

I observed colonies of *Parawixia bistriata* in the field (6 from dry sites, 16 from wet sites) to obtain estimates of the natural occurrence of group feeding within colonies. These data were collected between October 2001 and January 2002 of field season 1. Based on scan sampling (Lehner 1996) of each colony I estimated the frequency of group feeding for a colony as the proportion of groups of spiders feeding relative to the total number of feeding events (solitary and groups) observed for that colony. 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 five seconds to scan a linear meter of the sheet. Colonies were sampled at the beginning of the evening foraging activity period of *P. bistriata*, within the first two hours after the capture webs had been built.

Effect of the size of the prey 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 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). Data were collected during two seasons: between October 2001 and January 2002, and between October 2002 and January 2003. Trials started when spiders in the colony had finished spinning their webs (between 19:30 to 20:30) and finished between 00:00 to 2:00 when there were not intact focal and surrounding webs required to conduct more trials. Moths (mainly Noctuidae and to a lesser extent Sphingidae) were used 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 #PP-2060D). Moths were assumed to be palatable if spiders bit the item after its capture. Evidence from non-palatable moths comes from a species, probably a tiger moth (Arctiidae) exhibiting aposematic coloration (black and white) which was rejected by the spiders after biting during the capture.

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 exhibited 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 of release, 2) the focal individual was at the 6^{th} instar in age, and 3) at least four of its nearest neighbors were positioned in foraging mode at the hubs of their webs, and 4) the sheets formed by connected capture webs in an P. *bistriata* colony usually extend 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. These criteria reflect the following: 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 neighbors "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 Jr. 1998), I chose only 6^{th} instar focal individuals to control for ontogenetic effects in foraging behavior.

A moth was offered to a spider by holding one of its 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 lux Sony handycam model CCD-TR416.

To examine how spiders share prey relative to its size, I recorded the number of spiders participating in the capture of a given prey item, the maximum distance from which neighboring spiders came to join in capture or feeding, and the number of spiders feeding on that prey. (Capture webs do not overlap in *P. bistriata* colonies). 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). A spider was considered to be attacking a prey item when it approached the item and started biting or wrapping it. The number of spiders feeding on a given moth was defined as the maximum number of spiders observed feeding on the prey for more than a minute in the feeding sequence, which ended with complete consumption or with the partitioning of the prey into pieces. The maximum distance from which neighbors joined the foraging group was measured as the number of webs separating the focal individual's web from that of the furthest neighbor. Webs surrounding the focal web 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 neighbor spiders approach the foraging group in webs units gives an idea of how many territories individuals have to cross to join the foraging group in addition to the actual distance the spiders traverse.

To control for differences in web size of colonies from different habitat types, I compared the metric distances between the center 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 6 colonies in the wet sites (8 in Wet 1, 2 in Wet 2). Within each colony I completed between 2 - 6 trials depending on the size of the colony and thus number of potential focal individuals with corresponding neighbors.

An *a posteriori* estimate of inter-observer reliability on the number of spiders participating in the capture of a prey was obtained by having a 2nd observer score the videotaped prey sequences for group size counts during the period of capture. I performed a Spearman rank correlation between the second observer and the original counts made in the field by myself. 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 inter-observer reliability are probably an under-estimation of the likely level of agreement between observers recording the data in the field. Inter-observer 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% ($r_S = 0.88$, $N = 15$, $P < 0.01$).

Five trials were not included in this estimate and subsequent analyses because of the failure of the observer scoring from the taped sequence to individualize spiders in those sequences.

Interactions between the focal spider and neighbors during foraging

I also videotaped some of the foraging trials of the prey manipulation experiment described above to test for differences in the degree to which individuals from wet vs. dry sites engage in agonistic interactions during solitary vs. group foraging (N = 9 trials for each of the four categories: solitary and group foraging trials from each habitat type). These data were analyzed by sequential analysis (Bakeman & Gottman 1997).

In both solitary and group foraging trials, the trial started when I introduced a moth to the web of a resident spider and ended when it was feeding alone on the whole prey or on a piece of it. I recorded all the interaction between the resident (focal) and neighbor spiders using the animal focus method (Lehner 1996). I used individuals from different colonies in each trial (exception = two group trials from each of the two habitats, which were taken using the same colony, but probably involving different individuals). The data were recorded using a 0 lux Sony handycam model CCD-TR416. The size of the prey items offered had a similar distribution both in the group (mean ± S.E. [g]; dry: 0.09 ± 0.02; wet: 0.09 ± 0.01; df =1, 16, F = 0.00, P = 0.99) and solitary foraging trials (mean ± S.E. [g]; dry: 0.07 ± 0.02, wet: 0.05 ± 0.01; df =1, 16, F = 0.81, P = 0.38). The number of spiders feeding on the prey items offered was as follows (mean ± S.E.): dry habitat, 6.9 ± 3.1; wet habitat, 5.0 ± 2.7. The trials were recorded during the first field season from October 2001 to January 2002.

All occurrences of behavior patterns during group and solitary foraging were transcribed using the software Observer version 5.0.31 (Noldus Information Technology). The behavior patterns recorded were based on those defined by Hodge and Uetz (1995) for agonistic encounters in colonial *Metepeira* and on other behavior patterns previously recorded for *P. bistriata* during foraging (F. Fernández Campón, unpublished data). The list of behavioral patterns is shown in Table A1.

Data analysis

Occurrence of group feeding under natural conditions

The frequency data obtained from the observation of natural colonies permitted a Wilcoxon rank sum test comparison of the prevalence of group foraging in different habitats. I used the NPAR1WAY procedure from SAS software version 8.02 in the analysis (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 the size of the prey item on group foraging: tendency to attack prey and feed in a group

I performed logistic regressions (GENMOD procedure of 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 moth offered, in grams) was used as a continuous explanatory variable. Year (1^{st} and 2^{nd} field season) and habitat (dry and wet) were the categorical explanatory variables.

Effect of the size of the prey item on 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 had an effect on group size. As the data on the size of the capture and feeding groups consisted of small integer counts, they violated the assumptions of parametric statistical tests. I applied a generalized linear model with Poisson errors, a log link function and type III significance tests (Poisson regression) to these data using the PROC GENMOD of SAS version 8 (Stokes et al. 2000). Examination of the diagnostics (deviance and df) also indicated that the data were over-dispersed. The data were thus scaled using the deviance to improve the fit to the model (Stokes et al. 2000). In this case, the type III analysis is based on the *F* probability distribution instead of χ^2 distribution. I selected the model that presented the best fit to

the data using a likelihood-based χ^2 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 and habitat were the explanatory variables.

I performed a Poisson regression to test for habitat effects on the distance from which neighbors participating in the capture and feeding of a prey item came. This method was appropriate because 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. These data were under-dispersed; thus I scaled them using the deviance to improve the fit to the model.

In both logistic and Poisson regressions, estimates of the parameter vector β were computed for 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.

Behavioral interactions during foraging

I performed a one-way ANOVA to test for an effect of habitat on the frequencies of those behavioral interactions between the focal spider and the other individuals in the foraging group (Table A1), with habitat as a factor. I used the ranks of the frequencies because the data deviated from a normal distribution.

I used matrix generating software from The Observer to develop a pathway diagram describing the sequences of behavior involved in foraging. In the generated frequency matrices, behavioral elements appearing in rows represented the preceding behavior and those elements in columns represented the target or subsequent behavior. The transition matrices were summed over all individuals of 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. Path

diagrams representing behavioral sequences were developed using the adjusted residuals of behavioral transitions following Van den Berg et al. (1999). In the diagrams (Figs. A4-A7), I only used positive adjusted residuals (transitions occurring more often than can be expected if the distribution was random). Arrows connect significant transitions and the thickness of the arrows indicates the value of the adjusted residual (thin arrows $Z > 1.96$, medium arrows $Z > 2.59$, thick arrows $Z > 3.29$). In addition, to detect differences between groups of individuals from different habitat of origin group, means ± S.E. of the adjusted residuals were calculated for selected transitions and analyzed 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 no included).

In an attempt to examine the effect of the size of the prey on spider-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 (mean ± S.E.; dry: 0.05 ± 0.03, wet: 0.06 ± 0.01; $F_{1, 4} = 0.20$, $P = 0.67$) and the three largest prey items (mean ± S.E.; dry: 0.14 ± 0.02, wet: 0.12 ± 0.03; $F_{1, 4} = 0.64$, $P = 0.47$) were offered to individuals from dry and wet habitats. The number of individuals in the groups from dry habitat were as follows (mean ± S.E.): small prey, 7.0 ± 1.0; large prey, 6.0 ± 1.7 ; for groups from wet habitats: small prey, 3.7 ± 1.2; large prey, 3.7 ± 1.5. I also performed the same analysis for solitary foraging trials comparing the behavioral 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, $F_{1,4} = 0.10$, $P = 0.77$).

RESULTS

Occurrence of group feeding under natural conditions

Group feeding events occurred in 31 % ($N_{tot} = 16$) of the colonies in the wet sites and 83% ($N_{tot} = 6$) of colonies in the dry site, yet the proportion of group feedings relative to the total number of natural feeding events observed per colony did not differ between habitats (Wilcoxon test statistic = 87.50; $Z = 1.45$; $P_{exact\ test} = 0.15$; Table A2). While only

approximately 5% of all feeding events involved feeding groups, 26% of all individuals feeding at any given time were participating in group feeding (Table A2).

Effect of prey size on the tendency to attack and feed on prey as a group

Neither the date nor the time of the trial was correlated with the size of the prey offered (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 between temporal variables and prey size allows the rejection of the hypothesized confounded effect of time variables on the response of spiders to prey size.

The tendency to capture prey as a group increased with size of the prey (Table A3). Individuals from dry habitats were more likely to capture prey as a group than individuals from populations residing in wet habitats regardless of prey size ($\chi^2_1 = 5.28$, $P = 0.02$, $\beta_{\text{dry vs. wet}} = 0.56$, odds ratio = 1.75; Fig. A1) but no significant differences were found between years.

Similar to the occurrence of group capture, the proportion of trials in which group feeding occurred increased with the size of the prey ($\chi^2_1 = 48.08$, $P < 0.01$). However in this case, neither differences between years ($\chi^2_1 = 2.99$, $P = 0.08$) nor habitats ($\chi^2_1 = 1.22$, $P = 0.27$) were significant (Fig. A1).

Effect of the size of the prey on group size during capture and feeding

The numbers of spiders participating in group capture increased corresponding to an increase in prey size (Table A4, Fig. A2). Results from the Poisson regression also showed an interaction effect between prey mass and habitat type. Contrasts of the parameter estimates indicated that the increase in capture group size with prey size was higher for individuals from dry habitats ($\chi^2_1 = 4.79$, $P = 0.03$, $\beta_{\text{dry vs. wet}} = 1.10$, predictor value = 3.00; Fig. A2). Feeding group size showed the same trend: the number of feeders present in a group corresponded to prey size (Table A5). In this case, habitat differences were more pronounced, as indicated by a larger β, than for prey capture ($\chi^2_1 = 11.47$, $P < 0.01$, $\beta_{\text{dry vs. wet}} = 1.73$, predictor value = 5.62; Fig. A3). There were also differences in the size of the feeding groups between years. However, the responses of individuals

occupying dry vs. wet habitats did not differ between years (Dry $_{\text{2nd vs. 1st year}}$: $\chi^2_1 = 3.02$, $P = 0.08$; Wet $_{\text{2nd vs. 1st year}}$: $\chi^2_1 = 1.02$, $P = 0.31$). Thus, the significant effect of year did not affect the significance of habitat.

There were no habitat differences in the maximum distance neighbors traveled to join capture groups ($F_{1,66} = 0.00$, $P = 0.95$); only the size of the prey had a significant effect ($F_{1,66} = 32.17$, $P < 0.01$). In contrast, prey size and habitat had a significant effect in the distance traveled to feeding groups (prey size: $F_{1,81} = 14.05$, $P < 0.01$; habitat: $F_{1,81} = 14.85$, $P < 0.01$): the interaction between these two variables was not significant ($F_{1,81} = 3.63$, $P = 0.06$). Neighboring spiders participating 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]). There were no significant habitat differences on the distances between a focal web and its six adjacent webs (Table A6).

Interactions between the focal spider and neighbors during foraging

Comparison of the sequential analysis of solitary vs. group foraging showed that the sequence of behavior patterns involved in solitary foraging is a subset of behavior patterns occurring during group foraging (contrast Figs. A4 & A5). The first part of the behavioral sequence from orientation towards the prey (FocusPr) to the point in which the prey item is bitten by the focal spider (Bite) is almost identical in both solitary and group foraging trials from the two habitat types. The only difference is that plucking behavior was not observed during the course of group foraging at dry sites. In these trials, the focal spider orients towards the prey and immediately approaches the prey. The mean frequency of behavior patterns that occurred after the prey was bitten, such as Shake Web or Wrap Prey, did not differ between foraging modes (solitary vs. group) and habitats (Table A7).

In solitary foraging trials the behavioral transition Shake Web – Shake Web was significantly more frequent in trials with individuals from dry habitat than among 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, $P < 0.05$). All other behavioral transitions did not show between habitat differences.

Among group foraging trials, there was no habitat effect on the average frequency of behavior patterns involving interactions between the focal and neighboring spiders (Table A8). Only the behavior Leg Contact was significant despite high variability among trials involving foraging groups representing the same habitat type ($F_{1,16} = 4.37$, $P = 0.05$; mean ± SD, dry: 17.22 ± 13.59; wet: 6.88 ± 6.67). When comparing behavioral transitions, Bite - LegCont was significantly more frequent in trials involving individuals from dry habitat ($t_{15} = 3.31$, $P < 0.05$), while the transitions Bite - LookPl and LegCont - Pull Prey were significantly less frequent in these trials ($t_{15} = -2.44$, $P < 0.05$; $t_{14} = 2.18$, $P < 0.05$).

Sequential analysis results suggest that behavioral sequences differ when individuals representing a given habitat type forage on small vs. large prey items (Figs. A6 & A7). Behavior patterns reflecting high levels of aggressiveness (Table A1), such as Shake Web and Grapple, occurred between the focal and neighboring spiders from dry sites when foraging on small prey but not when feeding on large prey items (contrast Figs. A6 & A7). Note that in trials with small prey items the behavioral sequence is LegCont - Grapple - EatPiece. 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 because grappling in those sequences quickly followed it where Grapple occurred. Thus, the main difference between foraging groups from dry habitats feeding on small vs. large prey items is in the occurrence of grapple behavior 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, social interactions such as leg contact occurred only when foraging on small prey. In trials with large prey the sequence mainly involves looking for a place on the prey item to feed and some prey wrapping behavior. But there is no direct contact among individuals feeding. This could reflect the small number of individuals noted for foraging groups in the wet habitat. The size of the large prey items offered were double the size of a 6th instar spider (body length [mm]: mean ± SE; prey items offered = 20.18 ± 0.81, $N = 6$; 6th instar spider = 9.87 ± 0.1, $N = 113$).

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 in the sequence of behavior patterns. The behavioral sequence in these trials was similar to the generalized prey sequence predicted from the pooled sample of all foraging sequences (Fig. A4), *albeit* simpler. With one exception the sequence was: Focus Prey - Approach Prey - Bite - Wrap - Bite - End. Only those trials in which individuals from wet habitat were feeding on large prey are more complex: here the sequence Wrap - Freeze was significant but behavioral sequences involving Freeze as the preceding act (i.e., Freeze - Wrap and Freeze - Bite) were not significant.

DISCUSSION

This paper focuses on the foraging behavior of *Parawixia bistriata*, examining how resource levels and hunger stress affect social behavior patterns within a colony. I estimated the prevalence of group feeding in the field and conducted experiments to study the responses of individuals to changes in sizes of prey when under different hunger stress levels.

Despite between-habitat differences in prey availability, field observations of foraging events indicate that group feeding occurs with similar frequencies in both dry and wet habitats. Solitary feeding events predominate but approximately 25% of the individuals feeding at any given time are 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 a greater proportion 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 coming from longer distances in the dry sites. The differences between wet and dry sites are thus quantitative rather than qualitative ones.

The stronger response of individuals from dry habitats can result from the higher hunger levels experienced. In turn, this can increase the perceived benefits of a collectively captured prey for neighbors while it increases prey defensibility costs for the focal individual. 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; Uetz et al. 1982; Uetz & Hodge 1990; Riechert 1991), it is possible that the high prevalence of group capture results from a stronger pressure on the part of the neighbors under low prey levels compared to populations experiencing high prey levels.

In this respect, group foraging in *P. bistriata* 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*, and 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 also been reported for lepidopteran larvae (Fitzgerald & Peterson 1988). In groups of foraging fish and birds food defense 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. bistriata*.

Compared to other social species of spiders that exhibit group foraging, the existence of a foraging territory in *P. bistriata* results in competitive interactions in the form of interference during capture and feeding. Competition during foraging has been reported in other social spiders (*Stegodyphus mimosarum*, Eresidae, Ward & Enders 1985; *S. dumicola*, Whitehouse & Lubin 1999; Amir et al. 2000; *Anelosimus jabaquara*, Theridiidae, Gonzaga & Vasconcellos-Neto 2002). Although small prey items are consumed individually, interactions in the form of interference competition do not occur during access to prey. Once the prey has been subdued, competitive interactions in the form of scramble competition occurs as suggested by higher consumption rates and

differences in mass gain of individuals feeding in a group (Willey & Jackson 1993; Whitehouse & Lubin 1999; Amir et al. 2000). Instances of interference competition may occur when large individuals dislodge smaller ones from a prey item and take their feeding position as reported for *Stegodyphus dumicola* (Whitehouse & Lubin 1999). However, active defense of the prey items as shown in *P. bistriata* has not been reported previously.

In *P. bistriata*, the pressure exerted by neighbors is observed in the response of the resident which performs a high frequency of behavioral acts that signal rejection to the approach by neighbors (e.g., repetitive web shaking). Web shaking was most often observed in solitary foraging trials at dry sites. In addition, the comparative analysis of group foraging trials involving small vs. large prey items showed that focal spiders from dry habitats feeding on small prey items also signaled to neighbors with web shaking. In these trials, grappling followed the monopolization of a piece of prey by the focal spider. These types of behavior patterns of a higher aggressive level did not occur when focal spiders were feeding on larger prey, probably due to the inability of a single individual to defend such prey. It cannot carry it off or cover the prey item to prevent intrusion from neighbors after all. Large prey also tend to attract more neighbors to join in capture and feeding as these prey produce larger amplitude vibrations that travel further through the colony silk network. Individuals encountering a large prey item simply may be unable to stop the influx of other members of the colony that are attracted by the vibrations produced by the struggling individual.

De Carvalho Jr. (1998) argues that in *P. bistriata* group capture arose as a means to minimize costs of defense of large prey items. He based his argument on the presence in the feeding group of individuals that did not capture the prey but feed on it, and also in the increase in the frequency of agonistic interactions among individuals during group foraging after the prey has been immobilized. In my study, the results from the trials with solitary feeding and the effect of the size of the prey on the frequency of interactions during group feeding trials support de Carvalho's argument in that when costs of prey defense are high, there is an absence of agonistic interactions among individuals and this results in the capture of prey in a group.

Of all aspects of foraging behavior studied here, the tendency to attack and feed on prey as a group and the effect of the prey size on the number of individuals in the capture and feeding groups differed most consistently between the two habitat types. The consequences of these behavioral 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 if 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 can have an important impact in the growth and survival of the individuals under the lower prey levels found in the dry sites. Under natural conditions, there were proportionately more colonies in which group feeding occurred in the dry sites compared to wet sites and, as a consequence, the number of individuals involved in group feeding across all colonies from each habitat type was higher in dry sites. Therefore, the higher tendency to capture prey and feed as a group in the dry sites combined with the higher prevalence of group foraging in these sites gives support to the hypothesis that group capture and feeding could be in part responsible for the success of individuals from these populations.

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Appendix

Table A1. List of behavioral elements recorded in foraging trials used in sequential analysis (see text for explanation).

Interaction with	Behavioral element	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	-
	Eats 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	-
	PullPrey	Pulls from prey in order to either get a piece or take it elsewhere	-
	WrapPrey	Wraps prey with silk using leg pairs III & IV	-
Prey/Neighbor	Approach	Moving towards the prey or neighbor	0
	Focus	Orientation of the body towards the prey or a neighbor	0
	Freeze	Sudden cessation of movement in response to a movement/vibration	0
	Looks Place	Walks on prey or on other spiders feeding as if looking for a place to eat from the prey while touching prey or spiders with legs	0
	Walks Away	Walks away from the prey item or a neighbor spider.	0
Neighbor	Grapple	Grappling with other spider using the legs. No bites involved.	2
	Leg Contact	Touches other spider with first pair of legs	0
	ShakeWeb	Shaking the web using the front pair of legs. Usually performed in response to vibration produced by other spider, sometimes orienting the body towards the spider.	1

Table A2. Proportion of feeding groups and individuals participating in feeding groups relative to the total feeding events recorded per colony under natural conditions.

Proportion relative to all feeding events	Habitat	Mean ± SD	Coefficient of variation	*N*
Feeding groups	Dry	0.05 ± 0.04	0.71	6
	Wet	0.04 ± 0.09	2.04	16
Individuals in feeding groups	Dry	0.26 ± 0.17	0.65	5
	Wet	0.26 ± 0.11	0.41	4

Table A3. Generalized linear model analysis (PROC GENMOD; binomial distribution of errors and logit link) of frequency of trials in which group and solitary captures occurred.

Source	df	χ^2	*P*
Prey mass (g)	1	25.30	< 0.01
Habitat	1	5.28	0.02
Year	1	0.26	0.61

Deviance = 395.10 with 314 df.

Table A4. Generalized linear model analysis (PROC GENMOD; Poisson distribution of errors and log link) of capture group size (number of spiders participating in group capture) in dry and wet habitats.

Source	df	χ^2	*P*
Prey mass (g)	1	13.47	< 0.01
Habitat	1	0.12	0.73
Year	1	1.35	0.24
Prey mass x habitat	1	4.79	0.03

Deviance = 46.73 with 125 df.

Table A5. Generalized linear model analysis (PROC GENMOD; Poisson distribution of errors and log link) of feeding group size (number of spiders participating in group feeding) in dry and wet habitats.

Source	df	χ^2	*P*
Prey mass	1	14.43	< 0.01
Habitat	1	0.00	0.99
Year	1	6.37	0.01
Prey mass x habitat	1	11.47	< 0.01

Deviance = 148.82 with 127 df.

Table A6. General mixed model of the distance from a focal web to the six closest webs in dry and wet sites.

Source	Degrees of freedom		*F*	*P*
	Num.	Den.		
Adjacent web no.	5	394	21.34	< 0.01
Habitat	1	1.93	0.12	0.76
Habitat X Adjacent web no.	5	394	0.12	0.99

Covariance parameter estimates: Site(Habitat) = 24.09; residual = 164.39

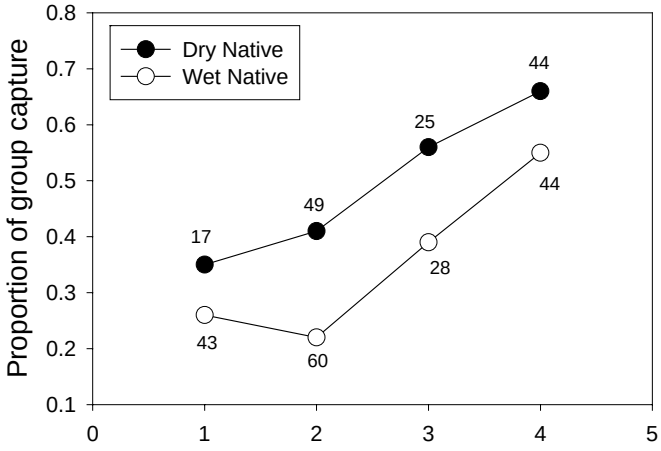
Table A7. Two-way ANOVA of ranked frequencies of behaviors occurring in all types of foraging trials with individuals from dry and wet habitat types.

Behavior	Source	Degrees of freedom		*F*	*P*
		Num.	Den.		
Shake Web	Foraging Mode	1	32	3.33	0.08
	Habitat	1	32	0.67	0.42
	Foraging Mode X 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 X Habitat	1	32	1.05	0.31

Table A8. One-way ANOVA of ranked frequencies of behaviors occurring in group foraging trials and the proportion of trials in which the particular behaviors occurred.

Behavior	Degrees of freedom		*F*	*P*	Proportion of trials in which behavior occurred	
	Num.	Den.			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

A.



B.

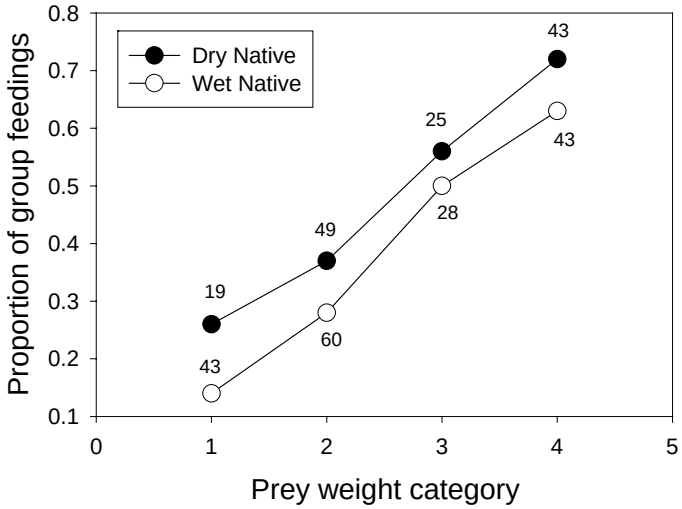
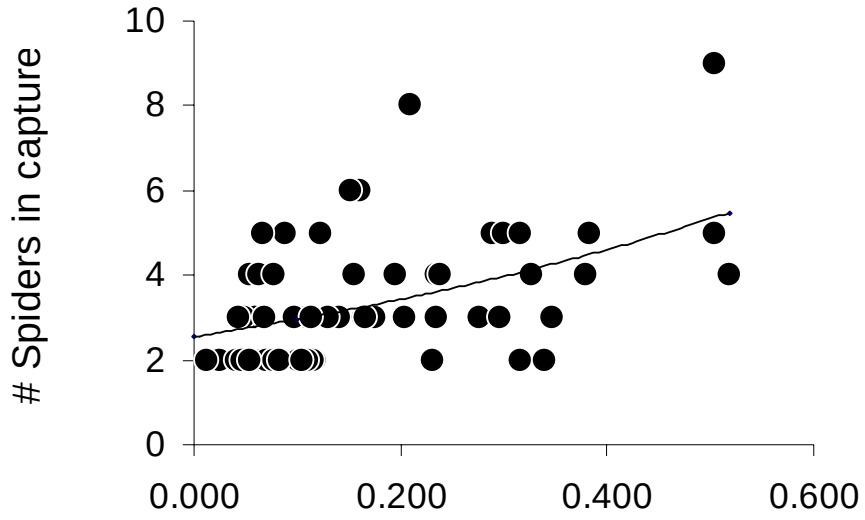


Figure A1. Proportion of group captures (A) and feeding events (B) as a function of prey size in dry and wet populations (numbers over circles indicate total number of trials per size class). Data on prey size were pooled into four prey size categories for graphic representation. Prey size categories were defined as a percentage of the average mass of a 6^{th} instar spider ($Mean_{6th}$ ± SE: 0.196g ± 0.005g, n = 215) as follows: category 1, 0-25%; category 2, 25.1%-50%; category 3, 50.1%-75%; category 4, > 75%.

A.



B.

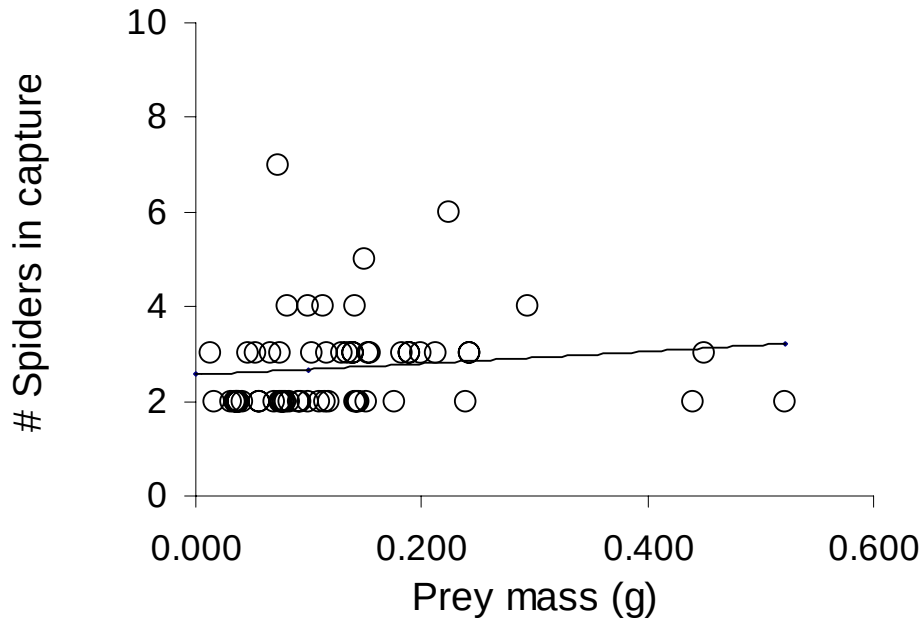
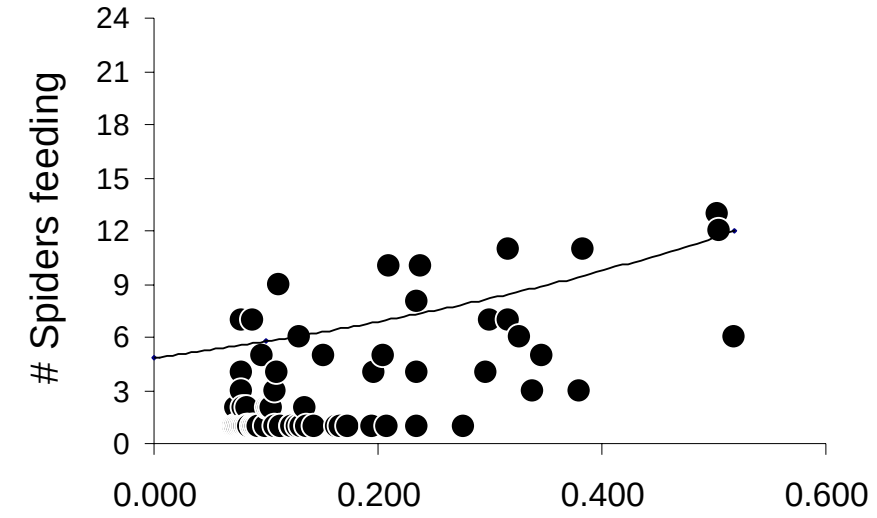


Figure A2. Number of spiders participating in group prey capture as a function of prey size. Functions plotted in the graphs are based on the estimates of parameters obtained for the Poisson regression described in table A4. For each of the groups, the equations were as follows: Dry habitat (A), $y = e^{(0.9204 + 1.4723\ x)}$; Wet habitat (B), $y = e^{(0.9408 + 0.4387\ x)}$.

A.



B.

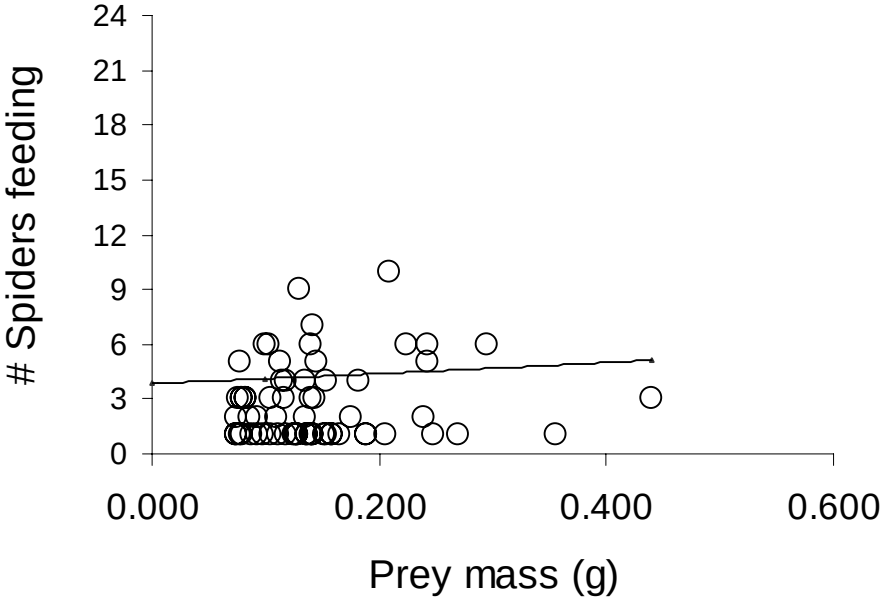
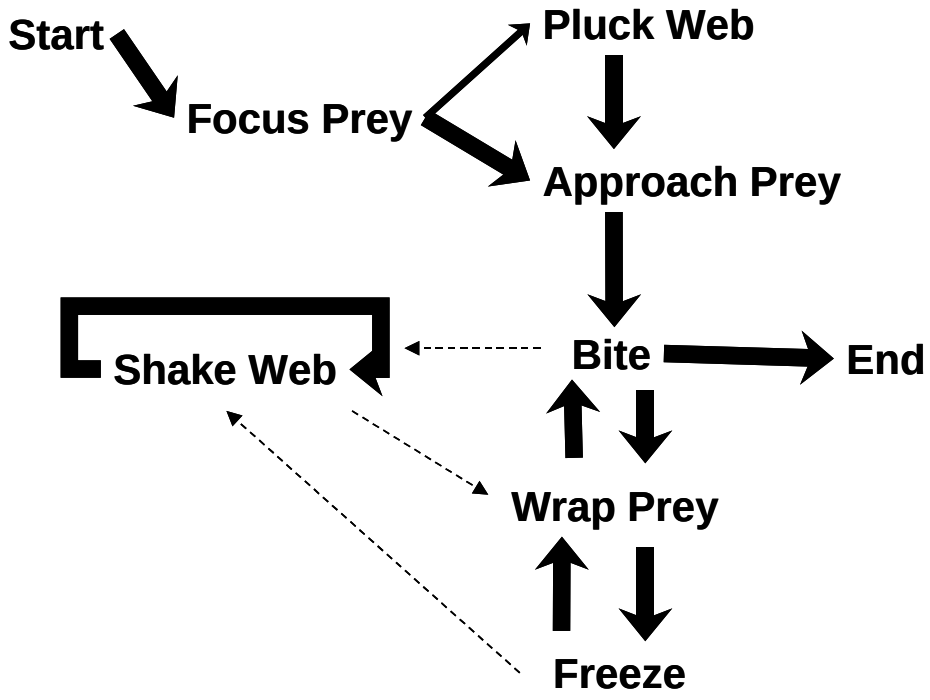


Figure A3. Number of spiders participating in group feeding as a function of prey size. Functions plotted in the graphs are based on the estimates of parameters obtained for the Poisson regression described in table A5. Equations corresponding to each group were: Dry habitat (A), $y = e^{(1.5759 + 1.7524\ x)}$; Wet habitat (B), $y = e^{(1.3497 + 0.6514\ x)}$.

Figure A4. Behavioral sequences during solitary foraging trials with individuals of dry (A) and wet (B) habitat types (see Table A1 for behavioral acts descriptions; LookPl: Looks Place, LegCont: Leg Contact; WalkAw: Walks Away). Arrows depict behavioral transitions; the thickness of the arrow refers to the value of the adjusted residual (Z) in the transition matrix (see text for explanation). The types of arrows shown are: thin arrows, $Z > 1.96$, $P < 0.05$; medium arrows, $Z > 2.58$, $P < 0.01$; and thick arrows, $Z > 3.29$, $P < 0.001$. Non-significant transitions are included to complete the sequences. These transitions are indicated by dotted lines. The non-significant transitions were included based on the highest transition probabilities.

A.


Start
Focus Prey
Pluck Web
Approach Prey
Shake Web
Bite
End
Wrap Prey
Freeze

B.

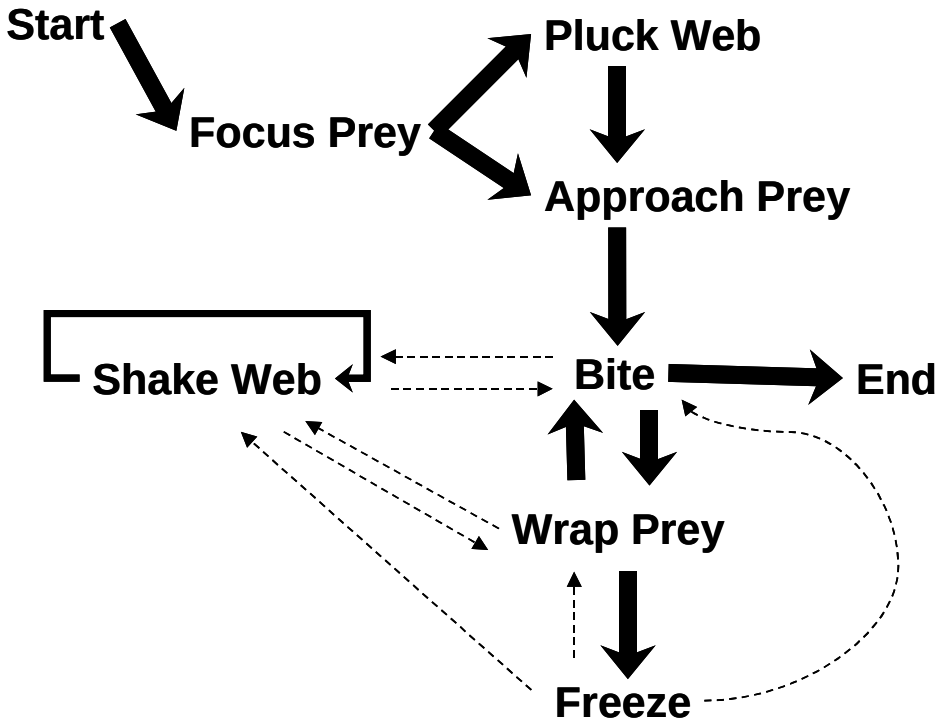
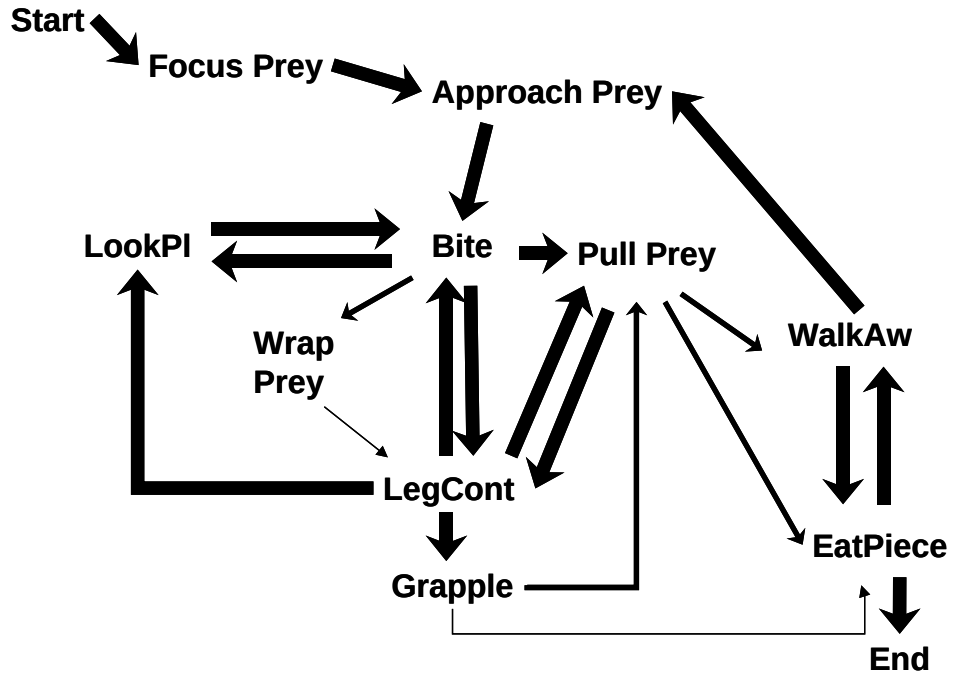

Start
Focus Prey
Pluck Web
Approach Prey
Shake Web
Bite
End
Wrap Prey
Freeze

Figure A5. Behavioral sequences during group foraging trials with individuals of dry (A) and wet (B) habitat types. Conventions as in Fig. A4.

A.


Start
Focus Prey
Approach Prey
LookPl
Bite
Pull Prey
Wrap
Prey
WalkAw
LegCont
EatPiece
Grapple
End

B.

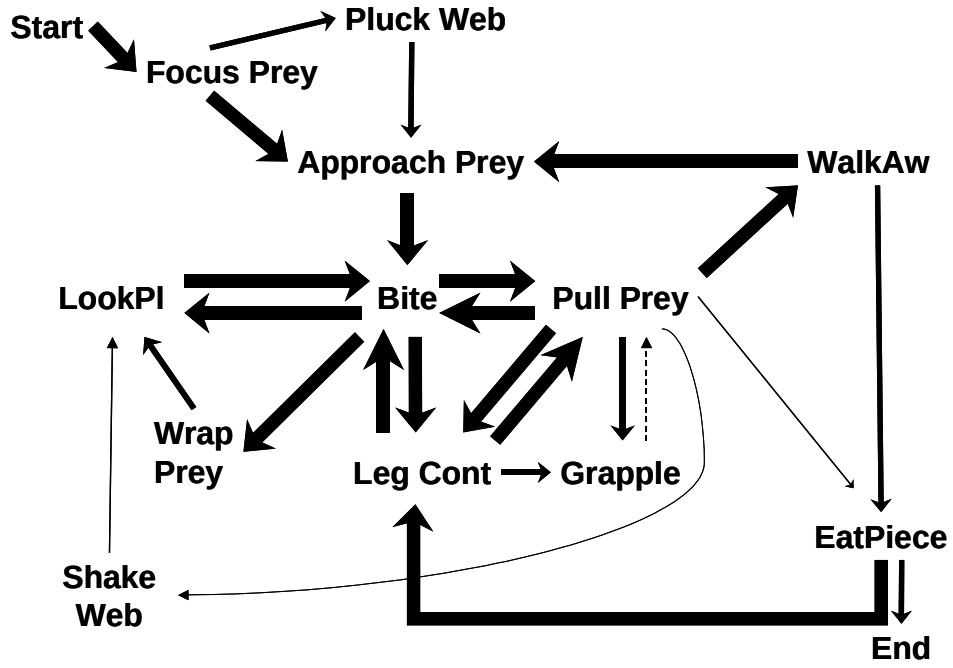
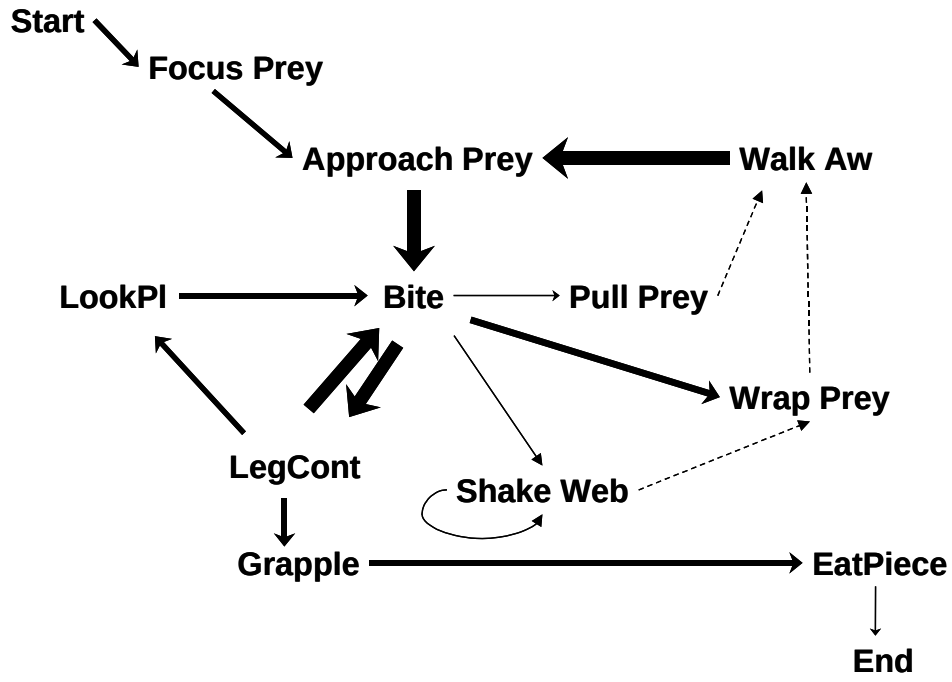

Start
Pluck Web
Focus Prey
Approach Prey
WalkAw
LookPl
Bite
Pull Prey
Wrap
Prey
Leg Cont
Grapple
EatPiece
Shake
Web
End

Figure A6. Effect of prey size in the behavioral sequences in group foraging trials with individuals from the dry habitat type. A) Trials in which small prey items were offered (mean ± S.E.[g]: 0.049 ± 0.033); B) trials in which large prey items were offered (mean ± S.E.[g]: 0.143 ± 0.022). Conventions as in Fig. A4.

A.


Start
Focus Prey
Approach Prey
Walk Aw
LookPl
Bite
Pull Prey
Wrap Prey
LegCont
Shake Web
Grapple
EatPiece
End

B.

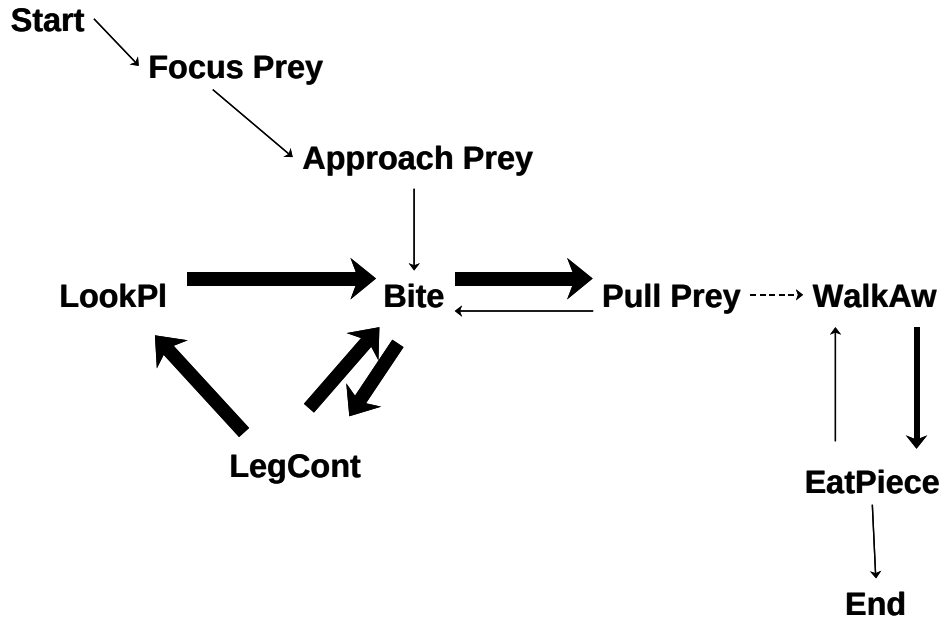
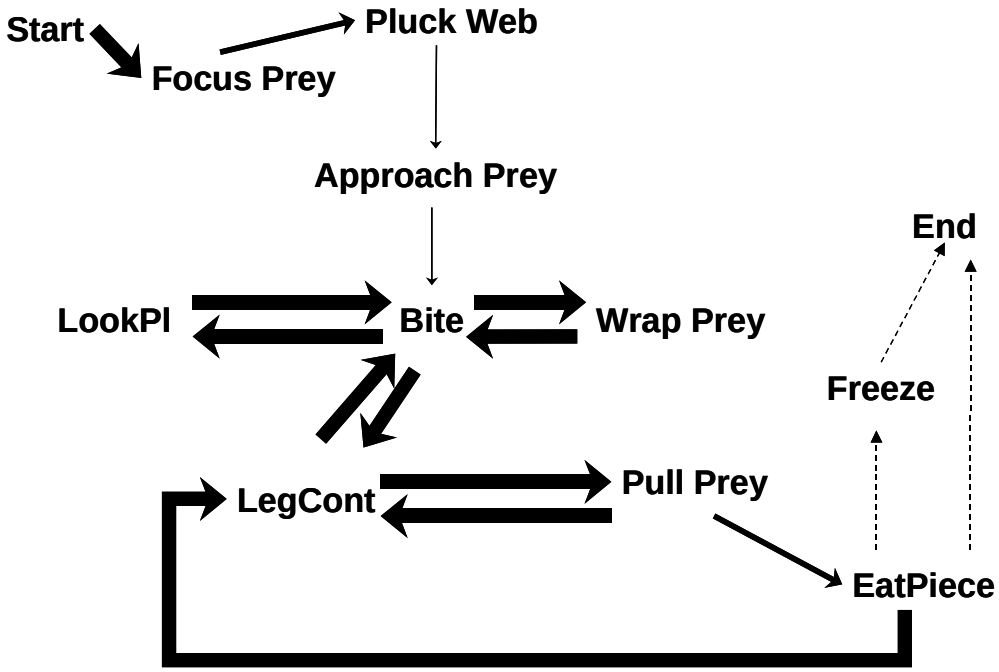
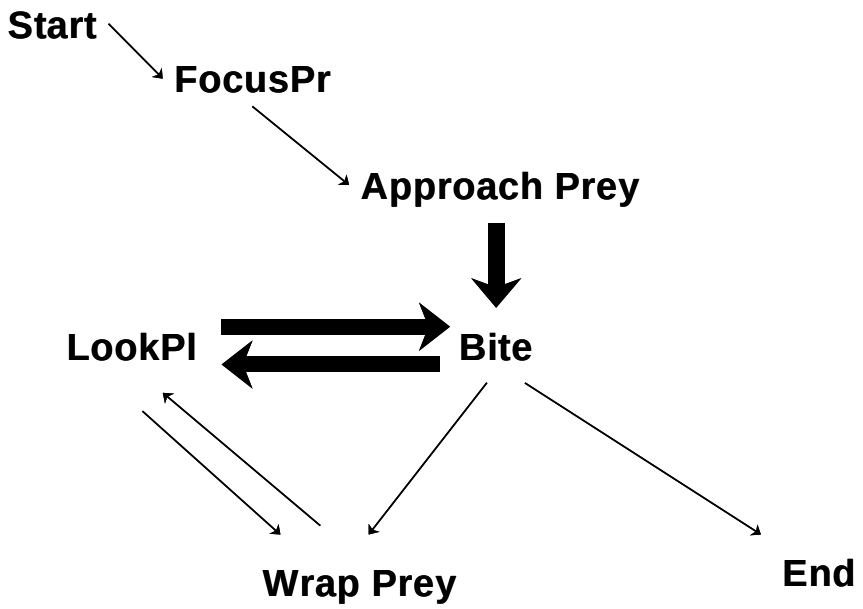

Start
Focus Prey
Approach Prey
LookPl
Bite
Pull Prey
WalkAw
LegCont
EatPiece
End

Figure A7. Effect of prey size in the behavioral sequences in group foraging trials with individuals from the wet habitat type. A) Trials in which small prey items were offered (mean ± S.E.[g]: 0.058 ± 0.014); B) trials in which large prey items were offered (mean ± S.E.[g]: 0.124 ± 0.033). Conventions as in Fig. A4.

A.


Start
Focus Prey
Pluck Web
Approach Prey
End
LookPl
Bite
Wrap Prey
Freeze
LegCont
Pull Prey
EatPiece

B.


Start
FocusPr
Approach Prey
LookPl
Bite
Wrap Prey
End

Part IV.

Environmental and genetic influences on between habitat variation in the foraging behavior of *Parawixia bistriata*

ABSTRACT

Using reciprocal transplant and prey manipulation experiments, potential genetic and environmental determinants of population differences in the foraging behavior of the colonial spider *Parawixia bistriata* are examined. 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* in low-prey habitats show a higher frequency of group capture of prey than the one observed in high-prey habitats. Larger feeding groups also occurred in low prey habitats. Data recorded included measures of the tendency to capture and feed in groups and the number of individuals feeding on a prey item. Population differences in the tendency to capture prey as a group in the transplant experiment results were found: native individuals from the low-prey habitat showed a higher tendency to exhibit group capture and feeding than individuals of the two transplants and the native high-prey habitat groups. Prey levels also led to differences in the size of capture and feeding groups. Because individuals of high-prey habitat origin transplanted to the low-prey site showed the same tendency to attack prey as in their native high-prey habitat, they represent an ecotype that lacks behavioral plasticity. On the other hand, individuals of low-prey habitat origin did show a plastic response. The behavioral plasticity exhibited by spiders of low-prey habitat origin is associated with higher variability in prey availability in their native habitat. The correspondence between plasticity in the expression of group foraging, particularly the higher tendency to forage in groups when prey levels are low with the success of individuals from dry habitat under these prey conditions suggests that group foraging behavior can have an important effect on the fitness of these spiders.

INTRODUCTION

Intra-specific variation in phenotypic traits, such as behavioral traits, can be the result of different selective pressures experienced by individuals over the set of habitats the species occupies. Both genetic and environmental sources can cause between population differentiations. On the one hand, population differences in behavior can reflect ecotypic variation through divergence where there is genotypic adaptation to local environmental conditions (Riechert 1999). On the other hand, these differences may reflect the ability of the genotype to produce different phenotypes under different environmental conditions (i.e., phenotypic plasticity).

It is possible to examine the sources of variation in behavior by conducting studies at the population level. Studies on geographic variation in behavior involve comparisons of the average phenotype expressed by individuals comprising those populations. The reaction norm is compared among populations to test whether the differences found are due to phenotypic plasticity or local adaptation. The reaction norm represents the mean phenotypic response of individuals of a population expressed under different environments. In order to compare reaction norms, it is necessary to subject genotypes to different environmental conditions. One way to test this is usually accomplished through reciprocal transplants.

The extent to which plasticity in a behavioral trait is favored in an organism depends on the relationship between generation time and the time 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 favored (Moran 1992). Alternatively, plasticity will be selected against in a stable environment if there are fitness costs to maintaining a plastic genotype. For example, there can be costs involved in acquiring information about the environment in order to respond in a plastic way (DeWitt et al. 1998). For example, if individuals exhibit plasticity in foraging activity in response to the presence of predators, being alert can inflict costs by decreasing the time available for other activities such as foraging. In an environment with no predators, alert individuals will spend less time foraging than individuals that are not

watching for a predator. Studies examining possible ways in which populations with plastic and non-plastic phenotypes arise have given support to the idea that plasticity predates non-plastic phenotypes. Based on different lines of evidence (neurobiology, genetic models) researchers have proposed that fixed phenotypic traits would evolve through genetic assimilation when there are fitness costs to maintaining plasticity (Tierney 1986; Mayley 1997; Schlichting & Smith 2002; Pigliucci & Murren 2003).

Spiders exhibit considerable plasticity in a number of behavioral traits associated with foraging. For example, web architecture has been show to be modified in the presence of predator cues (Li & Lee 2004) and can also vary with the type of prey encountered (Sandoval 1994). Tolerance among conspecifics has also been shown to vary in response to different rates of encounter with prey and prey size (Rypstra 1983, 1986; Uetz & Hodge 1990). Change in the foraging tactic according to activity prey levels has been shown in bolas spiders of the genus *Mastophora* (Araneidae). This group spiders use aggressive chemical mimicry to attract moth prey. Some species can change the proportion of pheromones produced in a blend with higher concentrations of the pheromome that attracts the moth species active at a particular time of the night (Haynes et al. 2002). However, population divergence in traits such as feeding territory size, predatory and anti-predator behavior have been shown in some spider species (Hedrick & Riechert 1989; Riechert & Hedrick 1990; Riechert 1993; Jackson & Carter 2001; Jackson et al. 2002).

The orb weaving spider, *Parawixia bistriata* exhibits similar fitness-related traits (number of eggs produced per sac) in populations that occupy habitats offering different prey levels (wet vs. dry), but it shows population variation in elements of its foraging behavior (Part III). In particular, individuals from wet habitats, with higher prey levels, exhibit a lower tendency to capture prey collectively as well as fewer participants in both capture and feeding groups than spiders from dry habitats where prey levels are lower. It is possible that behavioral plasticity underlies the observed population differences in the tendency to form foraging groups. If the behavioral differences exhibited by individuals were plastic, we would expect transplanted individuals to behave similarly to the natives in each habitat (have the same reaction norm). Plasticity in foraging behavior underlying

differences among individuals from different source plants has been shown in grasshoppers of the genus *Melanoplus* (Orthoptera: Acrididae, Thompson 1999). Larvae hatched from eggs collected in the field from plants differing in their quality as food source (source environment) were exposed to their source plant and a plant of different quality. Regardless of the source environment, the grasshoppers exhibited diet-induced behavioral plasticity that enhanced feeding performance on hard-plant diets.

An alternative explanation to the existence of behavioral plasticity is that the behavioral differences in foraging behavior observed between populations of *P. bistriata* reflect ecotypic variation with dry and wet populations exhibiting respective 'group foraging' and 'solitary foraging' ecotypes. Evidence of behavioral ecotypes in the spider *Agelenopsis aperta* (Agelenidae) has been provided by Riechert & Hall (2000) after performing reciprocal transplants of *A. aperta* from arid and riparian habitats. The authors describe the existence of fearful and aggressive behavioral phenotypes in each habitat type, which correspond to predation, and resource levels found in those habitats. Transplanted individual exhibited the same behavioral phenotype as in their native habitat, which indicates the absence of plasticity in their response towards predators and prey levels.

A third alternative is that individuals from dry and wet habitats have different levels of plasticity in behavior resulting from selection on the norm of reaction. Habitat differences in temporal patterns of prey availability can lead to different norms of reaction (Moran 1992). If prey availability exhibits more temporal variability in one type of habitat, a plastic reaction norm would be expected in such a habitat while a non-plastic one would be favored in a more stable habitat type. Although not in the context of foraging but of male mating tactics, this has been shown to be the case with soapberry bugs. Individuals from populations in with different levels of spatial and temporal variability in male/female ratio exhibit differences in levels of behavioral plasticity (Carroll & Corneli 1999). Individuals from populations from the more variable sex ratio environment were more plastic behaviorally with the expression of mate guarding behavior changing as a function of sex ratio. Individuals from populations with a stable

sex ratio, however, did not vary the extent to which they guarded 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 tendencies 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 semi-arid habitats in southern South America. Individuals defend their capture webs from conspecifics but they forage in groups depending on the size of the prey. Individuals forage solitarily when prey is smaller than the spider and in a group when the prey items are larger (Fowler & Gobbi 1988; de Carvalho Jr. 1998).

My analyses of behavioral sequences during solitary and group foraging events suggested 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 (Part III). 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.

Study sites

All study areas were situated in the Chaco region of north-eastern 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 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 due to human disturbance it was not possible to conduct experimental manipulations at the site Dry 2. Thus, this site only provided data on the foraging behavior of spiders at native colonies).

Both habitat types have a marked dry season in the winter and wet summers during which 80 to 90% of the annual precipitation occurs. Although the daily mean temperature regime is similar between habitat types, freezing days are more frequent and annual precipitation lower in the dry sites.

Variability in prey availability between sites

In previously described work (Part II) I collected the insect biomass data over three sampling periods for each site during the field season extending from October 2002 to January 2003. Each sampling period lasted between two to eight 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 ± S.E. [g]: Dry = 0.159 ± 0.018; Wet = 0.277 ± 0.037). Temporal variation in total prey biomass throughout the field season was not found to differ between sites. It is important to this study to learn whether wet and dry habitats differ with respect to the size class of insects that contribute the most to total biomass because prey size affects the expression of group foraging (i.e., Is there a greater representation of large biomass insects in the dry or wet habitat?). I assigned insects into size classes of 5 mm increments, with the last category grouping insects equal or larger than 30 mm in body length. Using the frequency of insects within each size class, I estimated the biomass per size class using the equation developed by Schoener (1980):

$W = 0.0377\, l^{2.21}$

Where *W* is the dry biomass of the insects in mg and *l* the body length in mm. I transformed body length measures for each insect to grams and then calculated total biomass for each of the size categories.

Experimental methods

Reciprocal transplant

I conducted a transplant experiment to determine whether the behavioral differences exhibited by the *P. bistriata* populations of respective wet and dry habitats had genetically diverged or exhibited plastic responses to varying prey availability conditions. The transplants were conducted in two stages, the second completed to augment sample sizes given the low colony establishment success achieved in the first transplant year. In the first stage of the experiment, one colony of wet origin was found to be established in November 2001 after transplantation to the site Dry 1 in June. Two colonies of a dry origin were transplanted to the site Wet 2. Early in December 2001 and I 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 in their 3^{rd} - 4^{th} instars. Data collection started after individuals had over-wintered in the dry site for a period of four months in mid October. The transplantation of dry colonies to wet sites was completed when individuals in colonies were at the 3^{rd} and 4th instars from a site located in the vicinity of Dry 1. Data collection started two months after transplantation (in mid December 2002). 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: 9; second year: 9); 11 colonies of dry site origin transplanted to wet sites (first year 2; second year 9); and six colonies of wet origin transplanted to one of the dry sites (first year: 1; second year: 5).

No transplants were made within the immediate vicinity of existing colonies (the minimum distance to a 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 had hoped to increase the probability of successful establishment in the novel environment. The transplant colony was prepared for the move by cutting the segment of

the branch where the retreat was located and placing it in a 1-liter plastic bottle that had been cut into two sections. The two sections were taped together for the move. Only the half holding the retreat was ultimately attached to a branch at the new site. (With the exception of two transplants, the spiders abandoned the retreat inside the bottle and built a new one nearby.) The transplanted retreats were placed on a branch close to the trunk of a tree and at a height between 1.5 to 2 m corresponding to the position observed in colonies comprised of individuals in their 3rd and 4th instars in the field (F. Fernández Campón pers. obs.; Sandoval 1987).

When transplanting colonies I did not control for the effect the disturbance caused by manipulation during colony transplantation and for 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, pers. obs.) 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 micro-site to where I transplanted them.

Effect of the size of the prey on group foraging

I conducted a manipulative experiment to quantify the effect of prey size on the tendency to forage in groups between October 2001 and January 2002, and between October 2002 and January 2003. Data on native individuals has been previously analyzed (Part III). Here, I include data on individuals from transplanted colonies to further examine the existence of genetic vs. environmental sources of variation in foraging behavior 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). Moths were used 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 #PP-2060D).

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 exhibited 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 of release, 2) the focal individual was at the 6^{th} instar in age, and 3) at least four of its nearest neighbors were positioned in foraging mode at the hubs of their webs. These criteria reflect the following: 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 neighbors "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 Jr. 1998), I chose only 6^{th} instar focal individuals to control for ontogenetic effects in foraging behavior.

I estimated the tendency of native and transplanted 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 by a solitary individual. To quantify the size of capture and feeding groups, I recorded 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 one-minute interval in the feeding sequence, which ended with complete consumption or with the partitioning of the prey into pieces.

Data analysis

Variability in prey availability between sites

In order to examine spatial and temporal variation in prey size distribution within and between sites I examined trap insect biomass per size class for each sampling period.

A distance matrix based on dissimilarities between samples was constructed from the insect data using Kulczynski's coefficient (Legendre & Legendre 1998). An ordination (non-metric multidimensional scaling, MDS; Legendre & Legendre 1998; Vázquez & Simberloff 2003) was then performed on the dissimilarity matrix to place trap samples in two-dimensional insect class space. This analysis was performed with the MDS procedure of SAS. I performed a correlation between each of the two coordinates of the space and the distances of each trap for each insect size class to determine which of the variables (biomass per each of the size classes) contributed more to each of the coordinates of the diagram.

I also conducted a permutation test to examine the potential dependence of pair-wise trap dissimilarity distances on habitat type, under the null hypothesis that distances between traps within the same habitat type do not differ from those between traps from different habitats. To test this hypothesis I constructed a matrix with the same dimensions as those of the dissimilarity matrix in which pairs of traps within the same habitat were represented by zeros and pairs from different habitats were represented by one (habitat matrix). I calculated the standardized Mantel statistic (r_M) to measure the independence of entries of the dissimilarity matrix from the habitat matrix. I randomly permuted the elements of one of the dissimilarity matrix and recalculated the statistic 10,000 times, then calculated confidence limits enclosing the least extreme values of the statistic. The permutation test was performed using the algorithm written in Matlab (The Mathworks 1999) by Vázquez (2003).

Tendency of spiders to attack and feed on a prey item as a group

I applied analyses to a dataset that included the frequencies of solitary and group foraging trials of individuals from both native and transplanted colonies during the two years of this study. I used the variables ‘habitat of origin’ and ‘rearing environment’ to examine whether the behavioral differences found in the native populations were due to environmental or ecotypic variation. The behavioral response measured was the tendency to attack and feed on a prey item as a function of its 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 exhibit a flexible response to group forage 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 their reaction norms with different degrees of plasticity shown in their behavior. Finally, finding that both main effects were significant but not the interactions would indicate that dry and wet populations exhibit similar levels of plasticity in the tendency to forage in a group but they differ in their reaction norms, with one population showing a higher tendency to forage in a group over all prey sizes offered. This will also be indicative of genetic divergence in reaction norms.

I analyzed these data with a logistic regression using the GENMOD procedure in SAS. Variables included in the model were group capture as the dichotomous response and prey mass (wet weight in g), year (2001-02 and 2002-03), 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.

Effect of the size of the prey item on the sizes 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 had an effect on the number of spiders participating in those groups 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 generalized linear model with Poisson errors, a log link function and type III significance tests (Poisson regression) to these data using the PROC GENMOD of SAS version 8 (Stokes et al. 2000). Examination of the diagnostics (deviance and df) indicated that the data were over-dispersed. The data were thus scaled using the deviance to improve the fit to the model (Stokes et al. 2000). In this case, the

type III analysis is based on the F probability distribution instead of χ^2 distribution. I selected the model that presented the best fit to the data using a likelihood-based χ^2 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

Multidimensional scaling

Fig. A1 shows the ordination of the contents of the traps at each sampling period based on the distribution of total biomass among insect size classes within each trap. The variability in the distribution of insect biomass in time and space differed between habitat types (Mantel test, r_M = -0.79; 95% permutation confidence intervals, -0.29 - 0.29). In Fig. A1 we can see that traps from the dry site showed higher variability in this parameter than traps from either wet site. The size class that contributed the most to coordinate 1 of the non-metric multidimensional scaling was 26-30 mm in body length (r_S = 0.36, P = 0.04, N = 34). Coordinate 2, on the other hand, reflected variation with respect to the insect size class 16-20 mm (r_S = 0.71, P < 0.01, N = 34). Both of these size classes included insects larger than 6th instar *P. bistriata* (mean ± S.E. [mm]: 9.87 ± 0.01, N = 113).

Tendency to attack and feed on prey as a group

The prey size that was offered showed no significant relationship with the date of the trial (r_S = 0.06, N = 544, P = 0.19). Diel trial time, 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: χ^2_1 = 0.01, P = 0.93). Thus, although larger prey tended to be offered earlier in the evening as shown by the significant negative correlation between prey size and time, the time when the prey item was offered did not have an effect on the occurrence of group foraging.

Results of the logistic regression for the proportion of group captures among native and transplanted colonies showed a significant overall effect of prey mass (χ^2_1 = 44.22, P < 0.01) as well as a significant interaction between rearing environment and habitat of origin (χ^2_1 = 8.64, P < 0.01; Table A1). Contrasts among the four treatment groups indicated that the tendency for spiders to attack prey as a group was significantly higher for native individuals in dry habitats than for the other three groups (χ^2_1 = 4.82, P = 0.03; Fig. A2; Table A2). Results on the tendency to feed in a group showed a significant effect of prey size (χ^2_1 = 81.65, P < 0.01) but no significant effect of habitat of origin (χ^2_1 = 0.06, P = 0.81), rearing environment (χ^2_1 = 1.84, P = 0.17) or year (χ^2_1 = 3.35, P = 0.07; Fig. A3).

In the analyses in which the two habitats of origin were tested independently, differences existed in the tendency to feed as a group between native and transplanted individuals of dry habitat origin. Native individuals from dry habitats showed a higher tendency to feed in groups than individuals transplanted to wet sites (prey size: χ^2_1 = 27.30, P < 0.01; rearing environment: χ^2_1 = 5.41, P = 0.02). Individuals of wet habitat origin, however, showed similar tendencies to feed in groups whether they were in their native habitat or transplanted (prey size: χ^2_1 = 51.02, P = 0.01; rearing environment: χ^2_1 = 0.00, P = 0.96).

Effect of the mass of the prey on group size during capture and feeding

There was a significant overall effect of the mass of the prey on the size of capture groups (Table A3). In addition, there was a significant interaction effect between prey mass, rearing environment, and habitat of origin, indicating that each category of individuals (i.e., wet natives, dry transplants to wet habitat) responded to prey size

differently. The results of the contrasts indicate that individuals from wet sites that had been transplanted to dry sites showed a significantly stronger response to increases in prey size than other classes of individuals (Table A4, Fig. A4).

In the feeding groups, the number of individuals was also found to increase with the size of particular prey items ($\chi^2_1 = 20.19$, $P < 0.01$), though individuals from the four treatment groups responded differently to increases in prey size (significant prey mass X habitat of origin X rearing environment effect; Table A5). Foraging group sizes of both native and transplanted spiders in the wet habitat exhibited a significant increase with an increase in prey mass (Table A6; Fig. A5). There was also a significant effect of year ($\chi^2_1 = 34.84$, $P < 0.01$) on the incidence of group feeding. Predictor estimates indicate 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 ($\beta = 1.97$, predictor estimate = 7.15, $\chi^2_1 = 11.04$, $P < 0.01$) was stronger than the year effect . In addition, to further examine whether inter-annual variability in group size affected rearing environment differences in the size of the feeding group as a function of the size of the prey I did multiple contrasts between data at each rearing environment during each year and found that group sizes within each environment type did not differ between years (Table A7).

DISCUSSION

The focus of this chapter is on the mechanisms underlying differences in foraging behavior noted between spiders from dry vs. wet habitats. One prediction tested was that individuals from both populations would exhibit plasticity in these behavioral traits. If the foraging characters measured were phenotypically plastic, I expected transplanted individuals to behave more similarly to the natives in the habitat to which they had been transplanted than to natives from the habitats from which they originated. Another hypothesis is based on the idea that the populations have behaviorally diverged. In this case, transplanted individuals would be expected to behave as they would in their native habitat. Finally, it is possible that plasticity in foraging behavior is favored in particular environments with populations exhibiting different norms of reaction.

The behavioral trait that showed divergence between populations from dry and wet habitats is the tendency to forage as a group. Population differences in the degree to which individuals engaged in group capture, in part, reflected divergence in reaction norms and, in part, represented a plastic response to local prey conditions (Table A8). While both dry and wet populations of *P. bistriata* exhibited some group foraging, the norms of reaction have diverged between them. Populations of wet habitat origin showed no significant context variability in their tendency to group capture prey. However, the dry habitat populations exhibited plasticity in this trait: they tended to feed in groups when resources were low, but solitarily when prey levels were high. This was evidenced in the case of dry habitat individuals transplanted to wet habitats. The transplants showed a lower incidence of group foraging in wet habitats where prey levels are higher than did individuals in their native dry habitat, which afforded lower levels of prey. Because no difference was observed in rates of group capture of prey between individuals of wet population origin in their native habitat and transplants to dry habitat, I conclude that the wet habitat populations of *P. bistriata* lack plasticity in this trait.

Clearly, reduction in the tendency to attack and feed on prey as a group appears to be advantageous at wet sites. Where encounter with prey is high, individuals probably obtain optimal feeding levels through solitary foraging. By doing so, they avoid the costs involved in group foraging, which include injury inflicted by large prey and agonistic interactions among individuals in the group.

Quantitative differences in the sizes of the capture and feeding groups were observed in both wet and dry populations in response to changes in the local environment. Regardless of their habitat of origin, individuals modified their responses according to local conditions (i.e., proximally hunger levels and ultimately prey levels). Thus, larger capture and feeding groups were found in dry habitats that offered lower prey levels.

The stronger response in individuals from dry habitats can result from the higher hunger levels experienced compared to wet habitats, where there are more prey available. Hunger might increase the perceived value of a prey item. In addition, 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). Hence, individuals in the dry habitat which experience higher hunger levels show a resulting higher tendency to participate in group capture.

The larger feeding group sizes relative to the capture groups are a consequence of the presence of individuals feeding from a prey item they had not captured (i.e., scroungers, Barnard & Sibly 1981). This difference was particularly important in groups from both native and transplanted individuals in the dry habitat. Groups of house sparrows behave in a similar way and show a higher tendency to scrounge when their reserve levels are low (Lendvai et al. 2004). Lendvai et al. (2004) showed that behaving as a scrounger provides less variable feeding rates than behaving as a producer by finding a food patch (or capturing prey) on its own. Thus, behaving as a scrounger would be a risk-averse tactic.

Risk sensitive foraging is an area worth exploring in *P. bistriata*. Previous work on colonial species of the genus *Metepeira* has shown that spiders behave in a risk-sensitive way (Uetz 1988; Caraco et al. 1995; Uetz 1996). Individuals utilize a risk-prone tactic and are found in smaller colonies or as solitaries when under low resource environments. Individuals of *Metepeira* benefit from being in a colony by an increase in the capture rate through the deflection of insects from webs first encountered to neighboring webs ("ricochet effect", Uetz 1989). However, contrary to what has been found in *Metepeira*, individuals of *P. bistriata* appear to exhibit a risk-averse strategy under low prey availabilities. I base this conclusion on the higher number of scroungers in feeding groups in dry habitats. Group foraging has not been observed in *Metepeira*. Unlike *P. bistriata*, *Meteperia* are unable to shift between producer and scrounger tactics.

Absence of plasticity in the tendency to capture prey and feed as a group in individuals from wet habitats

Absence of plasticity in populations from wet habitats can be due to an absence of genetic variability for plastic genes, for example, as a consequence of a founder effect. This might be the case if the wet habitats had been colonized by a small number of individuals coming from dry habitats lacking the plastic genes. On the other hand,

absence of a plastic response can be due to the cumulative effect of neutral mutation and random drift (Pigliucci 2001), assuming enough time has elapsed since colonization of wet habitats. A third alternative is the existence of costs to plasticity and the consequent selection against the plastic genotypes. If costs to plasticity exist, it is possible that a plastic genotype is not favored in wet habitats (DeWitt et al. 1998; Pigliucci 2001). Thus, if a non-plastic genotype produces the favored phenotype, such a genotype would be favored over a plastic one (Komers 1997). In *P. bistriata*, individuals that show a higher tendency to participate in group feeding are more responsive to vibrations produced by prey in a neighbor's web. There are costs involved in group foraging in the form of agonistic interactions among individuals and even when injuries are not inflicted, there is expenditure of energy in these interactions. If prey levels are sufficiently high that optimal feeding levels can be achieved through solitary capture, lower levels of response to neighboring web vibrations (a higher threshold response) would be favored under these conditions. The higher threshold to elicit a response to a prey would result in lower responsiveness to prey caught in a neighbor's web. Foster (1999) argues that shifts in the frequency of expression of behavioral patterns, or in the threshold levels of stimuli that elicit them are common mechanisms underlying between population differences in behavioral patterns.

A fourth alternative to the absence of plasticity in foraging behavior in population from wet habitats is that selection on a trait causes changes in the expression of a correlated trait, thus limiting the level of plasticity of the second trait. This has been reported in a European species of frog, *Rana temporaria* (Merila et al. 2004). Plasticity in the rate of larval development against different levels of risks of pond drying was compared among populations from southern and northern latitudes in Sweden. In particular, the costs of plasticity to individual size at metamorphosis was measured. An increase in the developmental rate results in smaller size at metamorphosis, which negatively affects fitness. Populations from northern latitudes were under stronger selection for large size at metamorphosis than individuals from southern latitudes because the shorter growing season in the north does not allow for compensatory growth after metamorphosis. The authors found a negative correlation between the level of plasticity

in the developmental rate exhibited by individuals from the different populations and the size they attained at metamorphosis. They argued that the stronger selection pressure on size at metamorphosis was limiting the level of plasticity in the increase in the developmental rate of individuals in northern populations as a function of pond dessiccation risk.

In *P. bistriata*, it is possible that selection for lower aggression levels or higher tolerance towards conspecifics leads to lower responsiveness towards prey. Some species exhibit correlated behaviors across situations or behavioral syndromes (Sih et al. 2004). These can be expressed as higher aggressiveness towards prey as well as towards conspecifics (e.g., the desert spider *Agelenopsis aperta*, Riechert & Hedrick 1993). Selection for higher tolerance and lower aggression can affect the tendency to forage in a group. This would happen if higher levels of tolerance led to a lower pressure on the part of the neighbors to enter a resident's web by avoiding escalation in the interactions that occur when a prey lands on the resident's web.

To evaluate whether costs to plasticity exist in *P. bistriata*, it is necessary to compare the relative fitness of plastic and non-plastic genotypes producing the same mean phenotype under the same environment (DeWitt et al. 1998). At the population level, it would involve comparing the relative fitness of native and transplanted individuals in the same type of habitat. Based on the results from this study, it seems that exhibiting plasticity to capture large prey in a group does not have any costs to fitness. Individuals transplanted to wet habitats exhibit similar fitness estimates (number of eggs produced per sac, Part II) to those of native individuals. 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 fourth instars and the transplantation experiment ended after the individuals had laid egg sacs. So it is possible that there are costs to plasticity that could be experienced at an earlier developmental stage or there are maternal effects expressed in the offspring of the transplanted individuals (less yolk content in the eggs negatively affecting offspring survival, Morse & Stephens 1996). These data are not available at present.

Impact of foraging behavior on the success of populations

Group foraging activity in *P. bistriata* partly results from the impossibility on the part of the resident spider to monopolize prey and defend its web and from the pressure exerted by the neighbors. In this respect, individuals from dry and wet populations seem to constitute different behavioral types, which affect the outcome of these interactions depending on prey availability and hunger level. Native individuals in the dry habitat showed a higher tendency to attack prey in a group than any of the transplants or natives in wet habitats. In dry habitats, where prey levels are lower and can limit reproduction, the higher tendency to forage as a group appears to correspond with success at reproduction. Whereas native individuals in dry habitats reproduced successfully, individuals transplanted to this habitat type failed to show an increase in the tendency to attack prey as a group and also failed to successfully reproduce under those low prey environments. Therefore, it is possible that successful reproduction under low prey level conditions could depend on extra energy obtained from prey captured as a group. In wet habitats with high prey conditions, it might be better to avoid the costs involved in group foraging (e.g., exploitative competition, enzyme and venom piracy, agonistic interactions within the group) and forage solitary. In addition, both dry to wet transplanted individuals as well as wet native spiders successfully reproduced in wet habitats indicating that local prey levels and solitarily attacks on these prey permitted successful reproduction under those conditions.

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Appendix

Table A1. Generalized 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 X habitat of origin	1	8.64	< 0.01

Deviance = 559.90 with 477 df.

Table A2. Contrasts of the interaction rearing environment X habitat of origin in the generalized linear model of the tendency to capture prey in groups for native and transplanted spiders. (See table A1).

Contrasts	β	Odds ratio ($C.I._{Wald\ 95\%}$)	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.

Table A3. Generalized linear model analysis (PROC GENMOD; Poisson distribution of errors and log link) of the size of capture group size (number of spiders participating in group capture) in native and transplanted individuals from dry and wet habitats.

Source	Degrees of freedom		*F*	*P*
	Num.	Den.		
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 X rearing env. X habitat of origin	3	166	2.61	0.04

Deviance = 67.41, with 166 df. Variance adjusted for under-dispersion using deviance. Groups used as reference were: a: wet habitat; b: wet origin; c: second season; d: wet native.

Table A4. Contrasts of the interaction prey mass X rearing environment X habitat of origin in the generalized linear model of the size of the capture groups for native and transplanted spiders. (See table A3).

Contrasts	β	Predictor (C.I.$_{\text{Wald 95\%}}$)	χ^2	*P*
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

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.

Table A5. Generalized linear model analysis (PROC GENMOD; Poisson distribution of errors and log link) of feeding groups (number of spiders feeding in a group) in native and transplanted individuals from dry and wet habitats.

Source	Degrees of freedom		**F**	*P*
	Num.	Den.		
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 X rearing env. X habitat of origin	3	175	18.42	<0.01

Deviance = 200.34 with 175 df. Variance adjusted for under-dispersion using deviance.

Table A6. Contrasts of the interaction prey mass X rearing environment X habitat of origin in the generalized linear model of the size of the feeding groups for native and transplanted spiders. (See table A5).

Contrasts	β	Predictor ($C.I._{Wald\ 95\%}$)	χ^2	*P*
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.

Table A7. Contrasts of the interaction prey mass X rearing environment X year in the generalized linear model of the feeding groups size for native and transplanted spiders.

Contrasts	β	Predictor (C.I.$_{\text{Wald 95\%}}$)	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 & Dry-2nd as reference groups. The model included the following variables: prey mass, habitat of origin, rearing environment, year, and the interaction prey mass X rearing environment X 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

Table A8. Summary of results showing the effect size (β) of each explanatory variable (without including the variable prey mass). The effect size of the tendency to capture and feed in a group represents the odds ratio while that of the size of the groups represents the parameter estimates.

Behavioral Pattern	Habitat of Origin	Rearing Environment	Origin X Environment
Tendency to group capture			1.30
Tendency to group feed			0.06*[1]
Capture group size		1.18*[2]	
Feeding group size		1.97*[3]	

*[1] this result reflects what was found in the analysis of separate datasets by habitat of origin revealed that effect. *[2] the contrast involving DD was marginally significant thus here I consider that both groups in dry habitat (DD & WD) differed from the two groups in wet habitat (WW & DW). *[3] the model indicated a significant interaction prey mass X habitat of origin X rearing environment but the contrasts showed that groups from different habitats differed significantly.

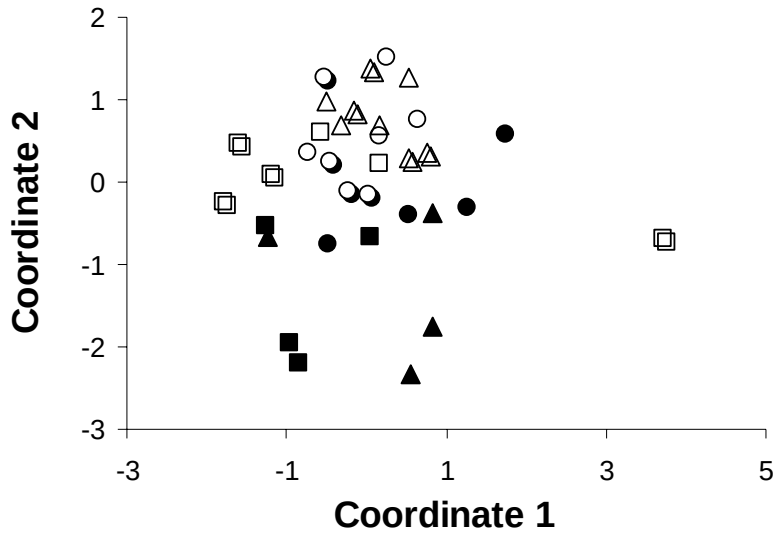
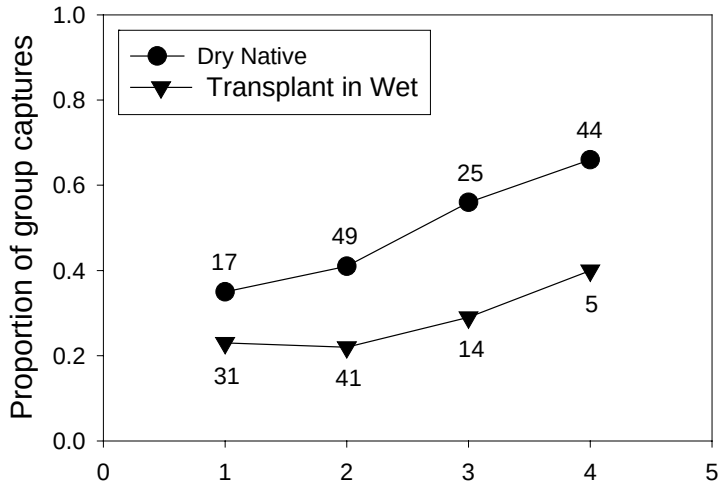


Figure A1. Reduced-plot of first two coordinates resulting from non-metric multidimensional scaling. Black symbols: traps in site dry 1; white with shadow: traps in site wet 1; white with no shadow: traps in site wet 2. The type of symbol represents the sampling period. Circles: first period; triangles: second period; square: third sampling period.

Figure A2. 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 was pooled into four prey size categories for graphic representation. Prey size categories were defined as a percentage of the average mass of a 6^{th} instar spider ($Mean_{6th}$ ± SE: 0.196g ± 0.005g, N = 215) as follows: category 1, 0-25%; category 2, 25.1%-50%; category 3, 50.1%-75%; category 4, > 75%.

A.


Dry Native
Transplant in Wet
Proportion of group captures
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
5
17
49
25
44
31
41
14
5

B.

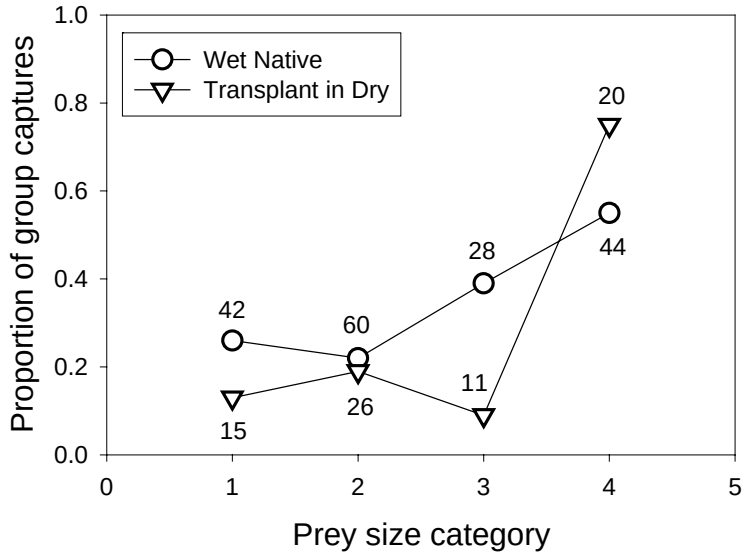
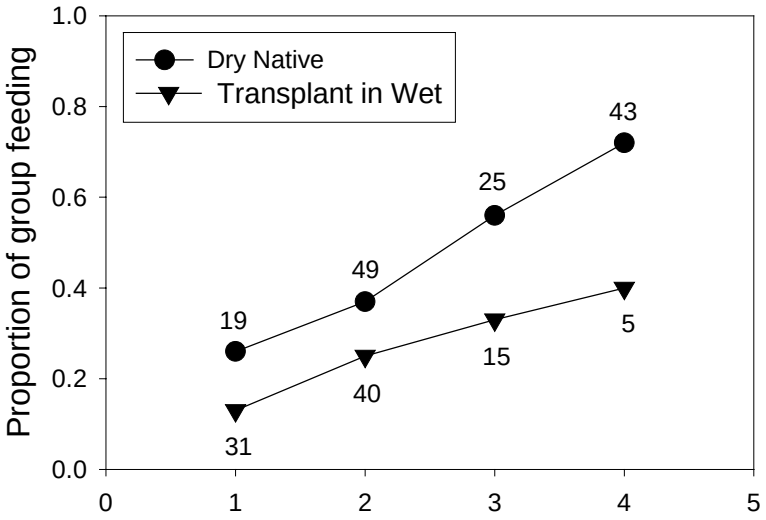

Wet Native
Transplant in Dry
Proportion of group captures
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
5
Prey size category
42
60
28
44
15
26
11
20

Figure A3. 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 was pooled into four prey size categories for graphic representation as in Fig. A2.

A.


Dry Native
Transplant in Wet
Proportion of group feeding
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
5
19
49
25
43
31
40
15
5

B.

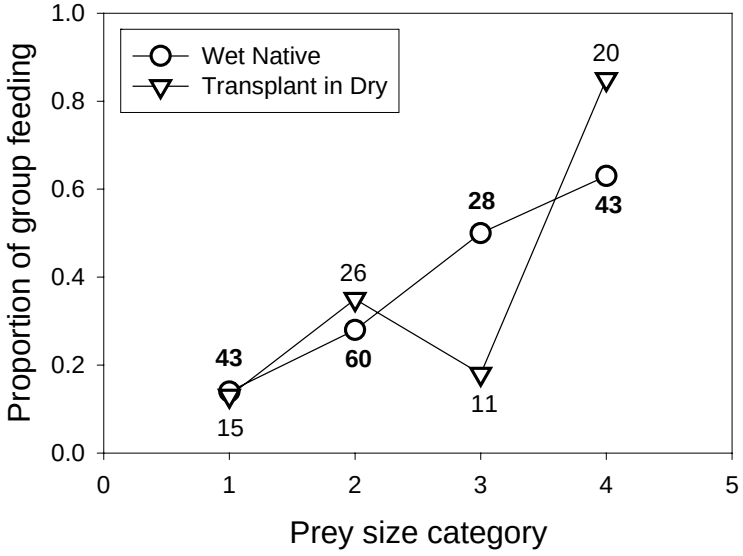
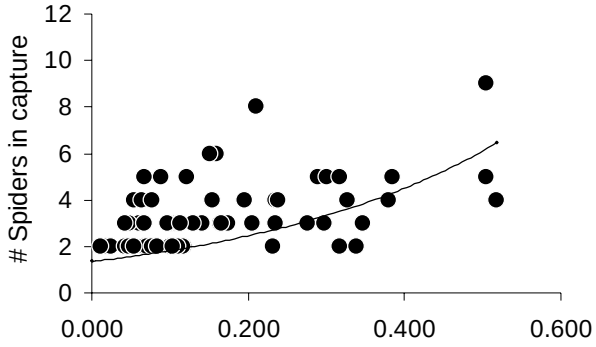
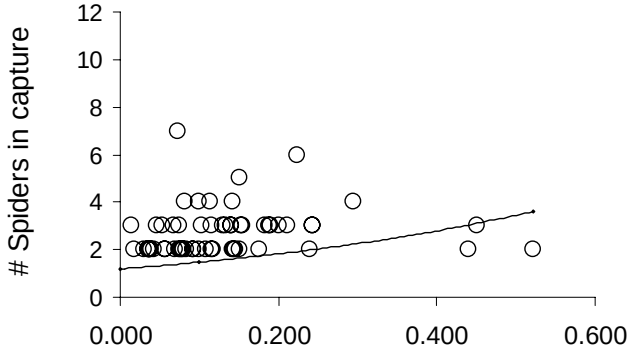

Wet Native
Transplant in Dry
Proportion of group feeding
Prey size category
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
5
43
60
28
43
15
26
11
20

Figure A4. 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 A2. For each of the groups, the equations were as follows: Dry Native, $y = e^{(0.3149 + 2.5886\ x)}$; Wet Native, $y = e^{(0.1783 + 2.1218\ x)}$; Transplant to wet, $y = e^{(0.3822 + 0.0798\ x)}$; Transplant to dry, $y = e^{(0.1110 + 3.9891\ x)}$.

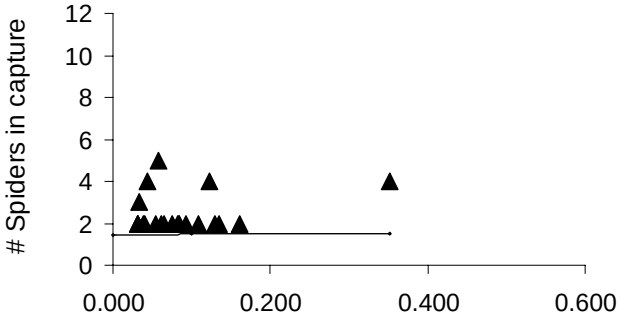
A.


Spiders in capture
0
2
4
6
8
10
12
0.000
0.200
0.400
0.600

B.


Spiders in capture
0
2
4
6
8
10
12
0.000
0.200
0.400
0.600

C.


Spiders in capture
0
2
4
6
8
10
12
0.000
0.200
0.400
0.600

D.

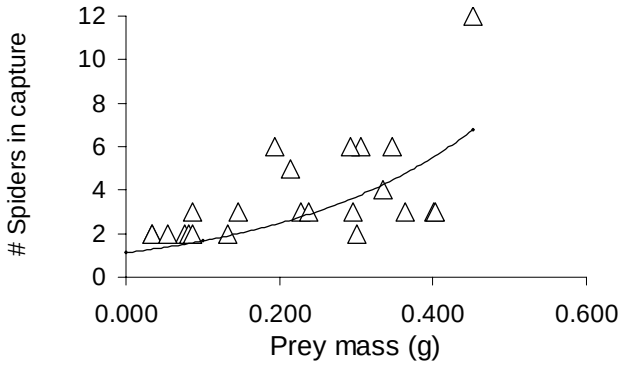
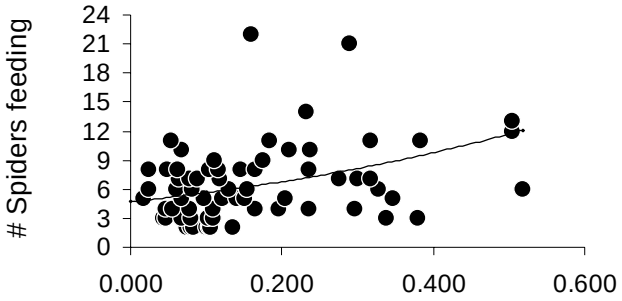
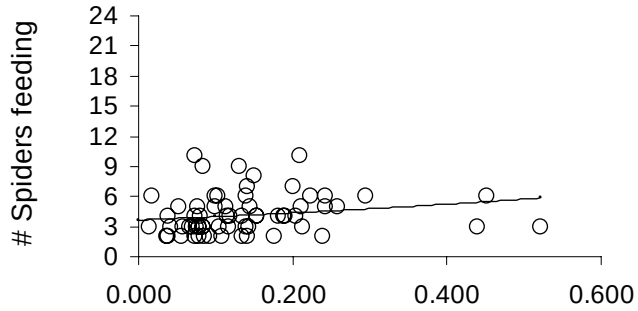

Spiders in capture
0
2
4
6
8
10
12
0.000
0.200
0.400
0.600
Prey mass (g)

Figure A5. 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 A3. For each of the groups, the equations were as follows: Dry Native, $y = e^{(1.5495 + 1.8244\ x)}$; Wet Native, $y = e^{(1.2936 + 0.9045\ x)}$; Transplant to wet, $y = e^{(1.5251 + 0.2315\ x)}$; Transplant to dry, $y = e^{(1.3180 + 3.1937\ x)}$.

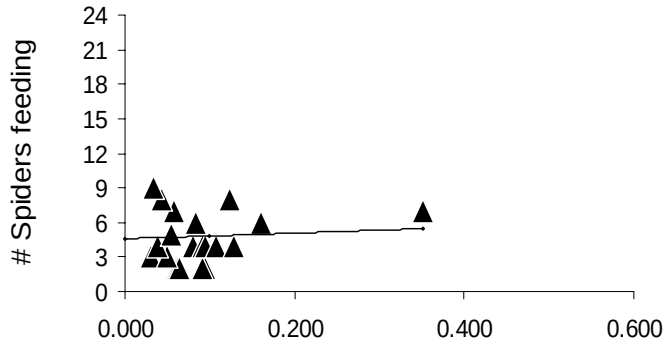
A.


Spiders feeding
24
21
18
15
12
9
6
3
0
0.000
0.200
0.400
0.600

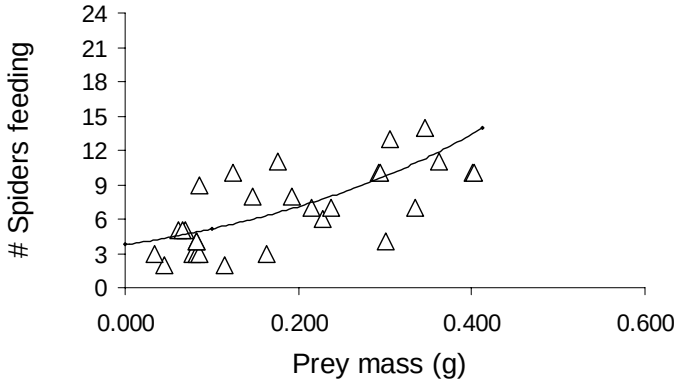
B.


Spiders feeding
24
21
18
15
12
9
6
3
0
0.000
0.200
0.400
0.600

C.


Spiders feeding
24
21
18
15
12
9
6
3
0
0.000
0.200
0.400
0.600

D.


Spiders feeding
24
21
18
15
12
9
6
3
0
0.000
0.200
0.400
0.600
Prey mass (g)

Part V.

Concluding remarks

In this study I examined geographic variation in life history and behavioral traits of the colonial spider *Parawixia bistriata*. I focused on variation in those social foraging traits that may have allowed *P. bistriata* to colonize habitats offering high vs. low prey levels. Differences in habitat utilization are not common in social spiders: most species are associated with high prey levels and most are in the wet tropics. This study of *P. bistriata* has provided insight into the mechanisms underlying its successful utilization of markedly different habitats and associated different resource levels. Specifically, I have identified some of the characteristics that adjust populations to different prey levels. These findings are unusual as they show that individuals participate in social activities more often when resources are low. Generally, spiders exhibit greater levels of aggression towards conspecifics in low-prey environments. This is because there is strong selection pressure for obtaining maximal feeding levels under limited encounter with prey (Riechert 1982, 1993, Riechert et al., 2001). This study thus provides a different perspective for conducting studies on social evolution in spiders. Below, I review the major results of this dissertation study, discuss the implications these findings may have for studies of the evolution of sociality and behavioral plasticity and suggest possible future lines of research on the *P. bistriata* system.

SUMMARY

In Part II, I showed that the phenology of populations differ between dry and wet habitats. In wet habitats, individuals of *P. bistriata* mature during the summer, while in dry habitats they mature in the fall at the end of the rainy season. The differences in phenology seem to result from the effects of low prey and possibly some abiotic factor such as temperature on the growth rate of juveniles. Spiders from both wet and dry populations of *P. bistriata* exhibited the environmentally induced changes in rates of development. Results from the transplant experiment showed that the inter-molt interval was a developmental trait affected by differences in local conditions. As a result the life cycle of individuals transplanted to dry sites was similar to that of natives from the respective environments. The absence of an effect of habitat on phenology of individuals

transplanted to wet sites could be due to the shorter duration of time they were in the novel habitat.

Also, in Part II, I showed that individual fitness (as estimated by the number of eggs produced per sac) differed between habitats. Generally, individuals from dry habitats achieved high fecundities in both native and foreign habitat, whereas individuals of wet habitat origin were less fecund in dry habitat than in their native wet habitat. In fact, most transplants from wet habitat failed to reproduce in the dry habitat.

The lack of a parallel response between traits associated with development and those associated with reproductive output indicates that there are other traits affecting fitness for which there has been population divergence. Population divergence in a number of fitness-linked, physiological and behavioral traits has been observed (e.g., resource allocation to reproduction in parasitoid wasps, Ellers & Jervis 2003; resistance to temperature stress in *Drosophila* species, David et al. 2004; levels of aggression and fear as found in the territorial spider *A. aperta*, Riechert & Hedrick 1993, or in the Atlantic salmon, Einum & Fleming 1997; and anti-predator behavior in the Trinidadian guppy, O'Steen et al. 2002). Any one of these traits can affect development and consequently adult size and fecundity. Thus, either differences in efficiency at allocating energy to growth or behavioral adaptations that increase the amount of food obtained would have an impact on fecundity through an effect on development. This latter effect was directly demonstrated in a quantitative genetic study Riechert & Johns (2003) completed on the link between behavioral aggressiveness and size in a desert spider. They demonstrated that aggression levels and adult size in *Agelenopsis aperta* are correlated. Aggressive individuals obtain and defend sites that have a greater foraging reward. As a result these spiders have a higher rate of survival, reach maturity more quickly and at a larger size than less aggressive individuals (Riechert & Johns 2003). The Riechert and Johns study was completed on spiders originating from a food-limited environment.

In Part III, I found variation among populations of *P. bistriata* in different aspects of foraging behavior. I observed differences between habitats in the tendency for individuals to capture prey and feed on it as a group as well as in the number of individuals participating in these groups. The analysis of behavioral interactions occurring during

both solitary and group feeding trials suggests that group foraging behavior is the result of pressure exerted by neighboring spiders and the impossibility of the resident spider to monopolize larger prey items that are more likely to be detected by neighbors. The agonistic nature of the interaction was evident in the acts performed by the resident spider in response to the intrusion (i.e., repetitive web shaking, which signals 'stay away'). Repetitive web shaking was most frequent in individuals from dry sites that were engaged in solitary foraging bouts. Other behavioral acts of higher aggression intensity, such as grappling, also occurred in feeding trials with individuals in dry habitats. This action pattern generally was followed by monopolization of a piece of prey with eventual solitary feeding by the resident spider.

The higher aggression levels observed in the behavioral sequences during the feeding trials with individuals from dry sites can be caused by the increased perceived value of a prey item when under low resource condition. Because this higher perceived value is experienced by both the resident and neighboring spiders, it apparently results in higher rates of group foraging in dry habitats. This is a consequence of the higher pressure exerted by potentially hungry neighbors to participate in the capture and/or feeding of a prey that has encountered an individual's web

In Part IV, I showed that of the traits exhibiting differences between habitats, only the reaction norm in the tendency to capture and feed on prey in a group actually showed between-population divergence. Individuals from dry habitat origin exhibited plasticity in this behavior, showing a tendency for group foraging in the dry sites where prey levels are low, while they tended to forage solitarily in wet sites with higher quantities of prey. In contrast, individuals from wet habitats failed to exhibit behavioral plasticity, showing low levels of group foraging regardless of resource levels. I argue that it is possible that if costs to maintaining plasticity exist, plasticity in the tendency to forage in groups may have been replaced by canalized behavior in populations under more stable conditions with higher resource levels.

Group foraging allows an individual under low resources to gain access to prey caught outside its capture web, its feeding territory. By intruding on the foraging bouts of neighbors, a significant proportion of individuals within a colony can profit from prey

caught on webs other than their own. This can also be of benefit to 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 with large prey by an individual spider is lower than that of 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. Therefore by participating in group foraging, *P. bistriata* seems to be able to exploit resources not available to solitary individuals and might experience a reduction in the costs of subduing large prey. Thus, we might expect that group foraging would particularly be favored in colonies experiencing low prey availabilities.

In conclusion, *Parawixia bistriata* exhibits between population variation in both life history and behavioral traits. Of all the traits examined, ecotypic variation was found only for the tendency to forage in groups. The correspondence between 1) plasticity in the expression of group foraging, particularly the higher tendency to forage in groups when prey levels are low with 2) the success of individuals from dry habitat under these prey conditions suggests that group foraging behavior can have an important effect on the fitness of these spiders. The ability of *P. bistriata* from dry habitats to adjust their foraging behavior from solitary feeding to group feeding under low prey conditions, permits them to achieve the level of reproductive success achieved by individuals from wet habitats where prey levels are higher and more uniform.

IMPROVEMENTS AND FUTURE DIRECTIONS

This work constitutes a first step at evaluating the conditions favoring the evolution of sociality in *P. bistriata* and more generally in colonial orb-weavers. Several questions have been raised from the findings of the study. For instance, there is the possibility that the more efficient use of prey achieved through group foraging is what allows *P. bistriata*

to occupy more arid habitats. This requires further examination, possibly by studying other groups with similar ecological characteristics to *P. bistriata* as well as other populations of this species under lower prey conditions. In this group it is necessary to examine if the observed correspondence between expression of the tendency to forage in groups and success of individuals holds.

A cost-benefit analysis to individual *P. bistriata* might also be completed. Estimates of group capture in populations from different habitats are necessary to understand the costs and benefits to individuals involved in group foraging. I have quantified the relative frequency of communal feeding in the field and noted that a significant proportion of individuals feeding at one time participate in communal feeding. I also experimentally demonstrated that the tendency of both group capture and feeding increases with the size of prey encountered and that group foraging is more likely to be exhibited by individuals originating in dry habitats under low prey availability conditions. I did not measure capture success rates for prey of different sizes by solitary individuals versus groups of various sizes. When discussing the results, I based my arguments on studies in other social species (Nentwig 1985; Ward & Enders 1985; Binford & Rypstra 1992), and I assumed that capture success of large prey is lower for solitary individuals compared to that achieved by a group of individuals. These measures are needed for the *P. bistriata* system. A complete analysis of the fitness consequences of group foraging would include the measurement of the following additional parameters: quantification of the investment in silk and venom during the capture of a prey, the risks associated with capture of larger prey (e.g., injury caused by prey or individuals of various sizes can consume) and consumption ability (meal size) for the individual spiders as function of its body mass.

The reciprocal transplant results suggest that group foraging is responsible for the success of individuals in dry habitats. Additional replicates are needed of the transplant experiment to adequately test this hypothesis. It is also important to have the appropriate control groups for the disturbance caused by the manipulation during colony transplantation. Native colonies should be transplanted within their site of origin to control for this type of disturbance. The effect of the disturbance caused by colony manipulation seems more important in the case of developmental data than behavioral

data. The latter was taken in transplanted colonies that had been established in the novel habitat for at least two months. Thus, probably after this period the effects of disturbance caused by manipulation of the colonies was negligible. However, an effect of manipulation disturbance cannot be ruled out until the appropriate controls are conducted.

Another aspect of the transplant protocol could also be improved on. I did not control for the exposure period in the novel environment. Thus transplants varied in the length of time they had been established and in the stage in the life cycle transplants were at. Perhaps two establishment treatments might be tested for the effect of experience: egg cases vs., for example, 3rd instar spiderlings that had some experience with the native habitat prior to transplant to the novel habitat. In the transplantation protocol followed in this study, individuals were transplanted when in their 3rd and 4th instars. Additionally, to eliminate any maternal effect present in the transplanted generation, a second generation should be tested. However, allowing the transplanted generation to reproduce in the novel habitat would increase chances of gene flow between native and transplanted individuals so caution should be taken to avoid that.

My transplant results suggest that dry habitat spiders transplanted to wet habitats do just as well as natives in terms of fecundity. Thus, there does not appear to be a fitness cost to the flexible foraging response spiders of dry habitat origin exhibit. Why does this arid phenotype not spread into the wet habitats? There may well be barriers to gene flow that impede the spread of the dry phenotype into wet habitat. But before considering this alternative, long term transplant studies are needed to identify potential costs to the noted plasticity. Once this is accomplished, evaluation of other alternatives such as barriers to gene flow would be pertinent.

This system would permit examination of potential trade-offs in resource allocation. In Part II I noted that, regardless of their habitat of origin, in the dry sites individuals produced fewer eggs per sac when compared to individuals reared in wet habitats (significant rearing environment effect in the analysis). This can be simply reflect the fact that low resource levels limit individual fecundity. It is also possible that the different selection pressures experienced in wet vs. dry habitats favor different clutch sizes, different egg sizes related to the amount of yolk added to the egg, and even differences in

silk investment in protecting the clutch. Increases in egg size at the expense of egg numbers occur (Berrigan 1991; Simpson 1995; Savalli & Fox 2002; but see Marshall & Gittleman 1994). For example, if larger egg sizes are favored in dry habitats, smaller clutches would be produced if there is a trade-off between size and number of eggs. In my study, egg sacs were collected and taken to the laboratory until eggs hatched. Thus, it was not possible to evaluate the survival of the progeny of spiders from dry and wet populations. Monitoring hatching success of native and transplanted individuals in the field and correlating it with measurements of egg size would allow us to determine whether differences in the reproductive effort of native and transplanted individuals were due to plasticity in reproductive strategy or a result of limited resources in the dry sites.

Another question arising from the study is related to *P. bistriata*'s ability to colonize new habitats. Phenotypic plasticity has been proposed as a trait facilitating colonization of new environments (Oliva et al. 1993; Grill et al. 1997; Madec et al. 2000; Yeh & Price 2004). When dispersing to a new habitat individuals encounter different environmental conditions, usually assumed to be harsher or, at least, unpredictable (Grill et al. 1997). In addition, studies examining possible ways in which populations with plastic and non-plastic phenotypes arise have given support to the idea that plasticity predates non-plastic phenotypes. Studies based on different lines of evidence (neurobiology, genetic models) have proposed that fixed phenotypic traits would evolve through genetic assimilation when there are fitness costs to maintaining plasticity (Tierney 1986; Mayley 1997; Schlichting & Smith 2002; Pigliucci & Murren 2003).

If plasticity in the tendency to forage in a group is the ancestral state and makes *P. bistriata* a good colonizer, we would expect to see populations coming from dry habitats colonizing wet habitats. In other words, if we could map the range expansion of *P. bistriata* through time we would expect to see ancestral populations in semi-arid environments and the more derived ones in wet habitats. However, finding ancestral populations in dry habitat would be opposite to the idea of having colonizers coming from more benevolent to more unpredictable habitats: individuals exhibiting plasticity in this study are from the dry sites, and dry habitats are more variable and offer harsher environmental conditions (e.g., lower prey levels, more extreme temperatures) than wet

sites. To examine which alternative explains *P. bistriata*'s distribution, it would be possible to conduct a phylogeographic study of populations of *P. bistriata* throughout its range tracking the history of colonization of the species (e.g., Masta [2000] on *Habronattus pugilis* [Salticidae] and recent dissertation work by Ayoub [2004] on *Agelenopsis aperta* [Agelenidae]). Later, it would be necessary to evaluate whether there is a relationship between the phylogeography of the species and the habitat types it has colonized throughout its history.

Agelenopsis aperta is predominantly desert spider but it also inhabits riparian areas distributed as patches throughout the arid land. *A. aperta* exhibits some similarities to *P. bistriata*. Both species occupy arid and more mesic habitats and both exhibit behavioral adaptations to differences in available prey levels. Previous work by Riechert and collaborators (reviewed in Riechert 1999) has shown that there are different behavioral types that correspond to desert and riparian habitats. Ayoub (2004) found that *A. aperta* populations inhabiting riparian patches were significantly different from each other as judged by mitochondrial genetic structure. This result indicates that the similarities in behavior found in riparian habitat are the result of independent natural selection, rather than a result of colonization history. In the case of *P. bistriata*, however, I would expect populations from the same habitat types to be more similar among themselves (as evaluated by neutral genes) than with populations from different habitat types. The distribution of semi-arid and mesic habitats within the range of *P. bistriata* is not patchy as in the case of *A. aperta*. Instead, there is a continuous decrease of precipitation levels from east to west in the Chaco region.

Other aspects of *P. bistriata* that can be examined further are related to its behavior. Although I analyzed the existence of competitive interactions during foraging, the analyses of the effect of the size of the prey needs further examination, mainly by increasing the number of trials examined. In addition, the existence of competitive interactions in the form of scramble competition during foraging remains to be documented in *P. bistriata*. This type of competition can lead to differences in mass gain of individuals participating in group feeding. In turn, this can be reflected in higher variability in the mass of individuals within a colony. In addition, it would be interesting

to examine how the extent to which group foraging occurs in a colony can potentially distribute resources more homogenously within the colony. The latter might counter-balance the effect that competitive interactions during foraging have.

Also, the behavioral tactics utilized by individuals during foraging can exhibit differences between populations. As noted briefly in Part IV, during group foraging there are individuals that feed from a prey item they had not captured (scroungers, Barnard & Sibly 1981). This phenomenon has been noted in other social species of spiders (Ward & Enders 1985; Gonzaga & Vasconcellos-Neto 2002) as well as other taxa which exhibit social foraging (Scheel & Packer 1991; Ha & Ha 2003; Lendvai et al. 2004). It was shown in house sparrows that hunger levels affect the tendency of individuals to behave as scroungers (Lendvai et al. 2004). In this study, the results from the size of the capture and feeding groups in the different rearing environments seem to agree with this effect of hunger on an increase in the scrounging tactic. However, it was also noted in Part III that competitive interactions during feeding might result in some individuals being excluded from a feeding group as the prey item tends to be monopolized. Thus, in addition to the effect of hunger, the probability of being excluded from a feeding group might affect an individual's tendency to use the catcher or scrounger tactics. Because competitive interactions in the form of interference were more common in individuals from dry habitats and a higher tendency to play the scrounger tactic was more prevalent when under low prey levels, it would be interesting to model how these two opposing factors affect an individual's foraging tactic. This model can be further tested in *P. bistriata* by quantifying the probability of being excluded from a feeding group as a function of group size, hunger levels and habitat of origin. While hunger level seems to affect the tendency to play the scrounger tactic in individuals from both habitats of origin, it is expected that the probability of being excluded from a feeding group would vary depending on the origin of individuals as indicated by the frequency of behavioral acts denoting interference competition.

Another question of evolutionary relevance is the extent to which genetic relatedness contributes to the evolution of sociality in colonial species. Cooperative spider species are highly inbred (Riechert & Roeloffs 1993; Avilés 1997), and this factor is assumed to

have contributed to the high sociality levels in this group of spiders and might also explain demographic characteristics (e.g., female-biased sex ratios, population dynamics). Uetz & Hieber (1997) suggest that because colonies of *P. bistriata* represent extended family groups, the high levels of relatedness would foster cooperation and could explain the use of a communal retreat and reduced territoriality in web-defense. It is possible that for *P. bistriata* high levels of relatedness relative to solitary species exist and this might have led to the higher tolerance levels among conspecifics that is required for sharing the retreat and communal threads supporting the webs. However, although one would expect *P. bistriata* to exhibit high levels of relatedness as colonies are mainly sibling groups, the fact that upon reaching maturity some individuals disperse and later mate suggests that some outbreeding occurs. Because *P. bistriata* is the only species within the genus reported to present any level of sociality, the genus does not constitute a good model for testing the idea of high relatedness as a factor facilitating sociality in orb-weavers. However, it is possible to conduct this type of test at the intra-specific level. Differences in relatedness can arise from differences in mating behavior among populations. This, in turn, might differentially influence the expression of social behaviors among populations.

There is very little known about the reproductive behavior of *P. bistriata* and other colonial spiders. In my study sites, I have observed mating of *P. bistriata* before and after dispersal. On the other hand, Sandoval (1987) reports that in populations in the Cerrado habitat mating only occurs after dispersal. How fast they reach maturity in the season and how much mass they have gained before dispersing might affect the reproductive decisions of individuals. For example, a female might reach a certain mass threshold for successful reproduction early in the season when males are still at the colony. In this situation, it could be advantageous to mate before dispersal, lay the egg sac at the colony, and then have a second mating attempt after dispersal. A male's chances of mating within the colony would probably depend on the reproductive status of females in the colony relative to females from other colonies that have already dispersed and become solitary. Another option that might function as an inbreeding avoidance mechanism is that males disperse from their natal colony to other colonies. While in social spiders this

phenomenon has not been documented, it has been reported in the eusocial naked mole rats *Heterocephalus glaber* (Rodentia; Bathyergidae; Braude 2000).

Questions about both the population genetic structure and reproductive strategies of individuals are related. A first approach would be to characterize the genetic structure of populations. In addition, quantification of inbreeding levels of eggs within clutches that have been deposited within a colony versus those laid by females after dispersal would provide some information on the mating system. In the populations included in this study, males disperse before females. However, in populations studied in the Brazilian Cerrado, females disperse first and colonies are comprised mainly by males at the beginning of the solitary stage (Sandoval 1987). These differences are probably reflected in the genetic structure of populations. Thus, in addition to the questions posed above, there are potential interesting questions to pursue in relation to the factors that might be causing the sexual differences in dispersal time in *P. bistriata*.

The large size of colonies and colony abundance in the landscape make the *P. bistriata* system a good one for field observations and molecular genetic studies. Pursuit of some of the questions address above, however, may be difficult to achieve using *P. bistriata*. As already noted, the completion of common garden and transplant experiments is difficult as the spiders tend to disperse when a colony is disrupted. Two solutions include a large number of repetitive transplants and the transplant of egg cases rather than juveniles. Another problem area is further investigation of the fitness consequences of group vs. solitary foraging. Group size would need to be manipulated and I have had limited success in completing such manipulations in the laboratory. Only a few individuals have constructed webs out of the 10-15 test subjects in lab enclosures. Perhaps providing more structure to which webs could be attached and smaller group sizes would meet with greater success. Capture group size in this study ranged from 2-12 depending on the treatment group and the size of the prey. Overall the average group size was three individuals. Feeding groups, on the other hand, ranged from 2-25 individuals with an overall mean of six individuals. It might be possible to work with smaller groups under controlled conditions if individuals are offered smaller prey that the largest prey items used in this study. In addition, if possible, prey items of discrete size rather than a

continuum of sizes may be used. This would facilitate the observation of the effects of competition during foraging measured as spiders mass changes when feeding on prey of different size.

Group foraging in *P. bistriata* can potentially increase in the amount of food obtained by individuals by allowing them to profit from prey landing on their neighbors' feeding territories. Based on the data from my study, native individuals from the dry habitats who showed higher tendency to forage in groups than the other native and both transplanted groups of individuals were successful at reproduction despite the lower prey levels found in dry habitats as compared to wet ones. Individuals transplanted from wet to dry habitat did not show an increased tendency to forage in groups and exhibit lower fitness estimates as measured by the number of eggs per sac produced by females. These results give support to the hypothesis that the expression of group foraging when under low prey conditions allows individuals to survive and reproduced in harsher environments. In this respect, *P. bistriata* differs from other colonial orb-weaver in which lower sociality levels occur in habitat where resources are lower.

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Vita

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