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Hunting Tactics in a Cobweb Spider (Araneae-Theridiidae) and the Evolution of Behavioral Plasticity

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Abstract Although behavior is being gradually incorporated into phylogenetic studies, the understanding of the evolution of one of its main characteristics, plasticity or adjustment to environmental features, is still a challenge, mainly due to the lack of comparative data. In this paper we focus on the plasticity of the predatory repertoire of *Achaearanea digitus*, analyzing its responses to two prey types, and discuss the evolution of behavioral plasticity based on a comparison to the foraging repertoire of other araneoid sheetweavers and on a review of hunting tactics among the larger group of orbweavers. Contrasting with what was observed for other families, spiders of the family Theridiidae (among them *A. digitus*) show a small set of attack tactics, and a quite stereotyped predatory performance. These spiders regularly attack their prey with a typical sticky silk wrapping tactic, but fail to use other tactics such as *bite–wrap* or *bite–pull out prey*, which are commonly used in other spider families. We show that this stereotypy is typical of the foraging repertoire of araneoid sheetweavers. Plotting the mean size of the attack tactics repertoire on the phylogeny of Orbiculariae shows that high predatory stereotypy is a plesiomorphy of the whole araneoidea group, and that evolutionary increases in plasticity occur independently two times in the group, among Araneidae and Nephilidae. The maintenance of a plesiomorphic, stereotyped predatory behavior among theridiids is probably due to the evolution of a special behavioral technique, which includes the simultaneous use of the fourth legs during *wrapping* attacks. Since the individuals in the species of this group of sheetweavers face less variable environments than do orbweavers, they should indeed evolve more stereotyped phenotypes, but nevertheless their evolved predatory stereotypy contrasts with plasticity in other aspects of their foraging behavior (web building). Since, in this case, both stereotypy and plasticity result

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from a simplification in the mechanisms underlying behavioral expression, we suggest that less variable environments select not exactly for behavioral stereotypy, but rather to the simplification of these information processing mechanisms.

Keywords Behavioral evolution · behavioral plasticity · behavioral repertoire · predatory behavior · spiders · sheetweavers · orbweavers

Introduction

Behavior is now being quite routinely incorporated into phylogenetic studies (Eberhard 1982; McLennan et al. 1988; Prum 1990; De Queiroz and Wimberger 1993; Paterson et al. 1995; de Pinna 1997; Scharff and Coddington 1997; Slikas 1998; Benjamin and Zschokke 2004; Kuntner et al. 2007), and objections to this practice are gradually fading. Nevertheless, the reasons behind these objections, that is, the variability of behavior as a response to environmental variability, have rarely been the focus of evolutionary studies (Atz 1970; Gittleman et al. 1998). While behavior seems to be generally more plastic than morphology, it is clear that some types of behavior are more stereotyped, while others are more plastic, and it has been pointed out the existence of different kinds of behavioral plasticity (Pigliucci 2001, p. 185). Some authors even argue that plasticity itself can be a selectable trait (Scheiner 1993; see review at West-Eberhard 2003), thus enhancing the need of an evolutionary approach to the study of plasticity (Gotthard and Nylin 1995).

One way to account for plasticity in an evolutionary perspective is through the concept of reaction norm (see Schlichting and Pigliucci 1998; West-Eberhard 2003, p.26), which can also be applied to behavior (Wcislo 1989). Reaction norms are a good tool to evaluate degrees of plasticity in one or few measurable aspects of behavior, but it becomes troublesome if we are to deal with variations in a whole repertoire of actions, or in a set of context-dependent, correlated behavioral responses. In this paper we make a distinct approach in order to grasp the variation inbuilt into large behavioral repertoires (see Japyassú and Viera 2002; Japyassú et al. 2006), taking as an example the predatory strategies of the spider *Achaearanea digitus* (Buckup et al. 2006), and further reviewing the literature on the plasticity of predatory attack tactics in the whole Orbiculariae clade (a group comprising all orbweb building spider families).

A. digitus builds a small cobweb (c. 10 cm of height) consisting of a retreat built into a leaf, and gumfoot lines spanning from the retreat to the litter below (Silveira and Japyassú 2002). Spiders of the genus *Achaearanea* are derived theridiids which have lost the colulus setae; their lost-colular-setae clade is sister to the one of the social spiders (*Anelosimus* spp., Arnedo et al. 2004). Theridiids build at least four different scaffold webs (Benjamin and Zschokke 2003), but the knowledge on web diversity and other behavioral aspects of this family is still scarce (but see Knoflach 2004 for an excellent account of theridiid courtship). They build two kinds of irregular webs with gumfoot lines (*Achaearanea*-type webs, with a small retreat, and *Latrodectus*-type webs, with a retreat inside an irregular mesh) and two kinds of sheetwebs (*Theridion*-type web, with viscid threads in the sheet, and *Coleosoma*-type webs, without these viscid elements, see Benjamin and Zschokke 2003). These webs are evolutionarily derived from sheetwebs without gumfoots (built by linyphiids). Griswold et al. (1998) name all these spiders "araneoid sheetweavers", a nomenclature that we will maintain throughout this paper. These araneoid sheetweavers are themselves derived from orbweb building ancestors (Griswold et al. 1998).

In the present study we describe the predatory repertoire of *A. digitus*. We do not intend to describe the whole set of predatory responses, because we consider this an unending task: predatory behavior is dependent upon prey type and size (Robinson and Olazarri 1971; Coddington and Sobrevila 1987; Edwards and Jackson 1993), previous experience with prey (Jackson and Wilcox 1993; Jackson and Pollard 1996), development (Edwards and Jackson 1994), hungriness (Persons 2001), quality of the web (Rypstra 1982); it can be indirectly affected by the presence of predators (Persons et al. 2001) and, if we consider web building as part of a foraging bout, can be influenced by spider state (Witt and Baum 1960; Benforado and Kistler 1973; Vollrath 1987; Eberhard 1988; Higgins 1990; Japyassú and Ades 1998; Sherman 1994; Venner et al. 2000) and a multitude of environmental factors (see review in Thévenard et al. 2004). It seems thus unreasonable to inspect predatory responses in all these contexts. In order to study the evolution of plasticity, we only need a comparable measure of plasticity among different taxa. We accomplish this by measuring plasticity as a function of two prey types, controlling some major variables, such as spider hungriness, stage of development and sex, as well as web condition and prey size. We compare this data with that of other araneoid sheet and orbweavers studied under this same experimental setting (see Garcia and Japyassú 2005; Japyassú and Jotta 2005).

Although spiders are usually known for their behavioral stereotypy, there are some sparse clades where predatory plasticity could have appeared independently, such as among salticids (Jackson and Hallas 1986; Jackson 1990; Jackson and Wilcox 1993; Jackson and Pollard 1996), pholcids (Jackson and Brassington 1987; Japyassú and Macagnan 2004) and araneoid orbweavers (Robinson 1969; Robinson 1975; Robinson and Mirick 1971; Robinson and Lubin 1979; Robinson and Robinson 1973), thus providing an opportunity for testing hypotheses about the evolution of plasticity. The Orbiculariae clade is an interesting model group in this regard, since it contains the majority of the well studied versatile predators, side to side with some well known stereotyped hunters (Carico 1978; Binford and Rypstra 1992; Japyassú and Jotta 2005; Garcia and Japyassú 2005), all of them embedded within a known phylogenetic structure (Griswold et al. 1998). There is an abundant literature on the predatory behavior of araneoid spiders (for example, Ades 1972; Lubin 1980; Viera 1994; Japyassú and Viera 2002) and, more specifically, on the details of the attack tactic, the specific sequence of behaviors employed to subdue the prey. It has been shown that there is considerable plasticity in this tactic due to variability in prey taxa. As an example, the common garden spider *Argiope argentata* can subdue alternative prey (butterflies, grasshoppers, flies, etc.) with at least five distinct tactics, such as *bite–wrap*, *wrap–bite*, *bite–pull out–wrap*, *bite–pull out–carry–wrap* (delayed wrap) or out of web *bite–wrap* (Robinson 1969; Robinson and Olazarri 1971; Ades 1972). In the present paper we investigate the evolution, not of any particular attack tactic, but of the level of plasticity of these tactics. To accomplish this, we review the literature on predatory behavior and plot this data on the phylogeny of the group.

In order to discuss the evolution of the degree of plasticity built into complex, context-dependent behavioral strategies, we compare these results with recent hypothesis that advocate that spiders in this group have lost behavioral stereotypy (Benjamin and Zschokke 2004; Eberhard 2000). We conclude that the apparent contradiction between these authors and the present paper can be resolved if we take into account the existence of different kinds of behavioral plasticity.

Methods

Forty adult female *A. digitus* specimens were collected in a tropical 102.100 m^2 forest reserve, at the Cidade Universitária Armando Salles de Oliveira (CUASO-USP). The specimens were kept in acrylic boxes (15×15×15 cm). Each individual was fed once a week with live crickets (*Gryllus* sp.) of size similar to the spider's body length. Voucher specimens were deposited in the collection of the Instituto Butantan, São Paulo (curator A.D. Brescovit) with the numbers IBSP (33210; 33214–33216; 33218–33220; 34865–34870; 34872–34877; 34879).

Behavioral Data Collection

The predatory sequences were videotaped (miniDV Canon XL1 camera). In order to evaluate the plasticity of the predatory repertoire, we gave ant workers (*Atta* sp.) to 20 adult female spiders, and beetle larvae (*Tenebrio molitor*) to another set of 20 adult females. Since relative prey size alters the details of the predatory sequence (Japyassú and Viera 2002), prey size was in all cases similar to spider body size (cephalothorax+abdomen). Although we did not explicitly control for prey weight, there were no significant differences between the weight of tenebrio larvae and ants ($N=28$; $Z=-1,836$; $P=0,066$).

Ants are an usual item in the diet of theridiids (Holldobler 1970; Carico 1978; MacKay 1982; Nyffeler and Benz 1987; Nyffeler et al. 1988; Breene et al. 1989, 1993; Nyffeler 1999), but this is not the case of tenebrio larvae, since worm-like prey is not usually in the diet of web based, sit-and-wait predators, such as *A. digitus* (Nyffeler et al. 2001—reviews the araneological literature showing that spiders sometimes feed on worms, but that only cursorial spiders do it). The use of a rare prey item, such as tenebrio larvae, allowed the measurement of aspects of behavior not influenced by previous experience with this specific prey type.

Since the density of web lines can alter prey capture efficiency (Rypstra 1982), and considering that spiders periodically add gumfoot lines to the web (thus changing the density of web lines, Benjamin and Zschokke 2002, 2003), all specimens were videotaped 15 to 30 days after web construction. To reduce the effect of the degree of starvation over the spider hunting behavior (see Herberstein et al. 1998; Persons 2001), each individual was videotaped after 1 week starvation period.

Each taping session began immediately after the prey adhered to a gumfoot, and finished 5 min after the spider transported its prey to the retreat. The session could also be interrupted after a 5 min sustained *bite*; this was done because after this long *bite* the spider usually was already feeding upon the prey. Alternatively, the session could be interrupted after a 15-min *pause*, since after such long *pauses* the prey usually was rejected.

Behavioral Sequence Analysis

Before videotaping the sequences, there was a phase of observational training where the spiders were observed capturing a variety of prey taxa. The videotapes were transcribed to a computer file using Observer Video-Pro 5.0 (Noldus et al. 2000). The behavioral categories used to decode spider behavior were described previously by many authors (Robinson and Olazarri 1971; Jackson and Brassington 1987; Viera 1986, 1994; Groppali and Senna 2000; Japyassú and Viera 2002), and are presented and discussed in the Appendix.

The predatory sequence was divided in three phases (adapted from Viera 1986, 1994). The detection phase encompassed the behaviors performed from the beginning of the sequence to immediately before the first sswrapping (wrapping with sticky silk). The immobilization phase started with the first sswrapping and ended when the prey is carried to the retreat. Finally, the feeding phase comprised the last 5 min of each sequence, with the prey immobilized at the retreat.

Statistical Analysis

Due to the departure from normality in the frequency of some behavioral categories, non-parametric statistical tests were used when necessary. To evaluate differences between prey types in the duration of the predatory sequence or in the overall frequency of behavioral categories Mann–Whitney U test was used. If there was a difference between the experimental treatments, a Canonical Discriminant analysis was used to detect the behavioral categories which most contribute to this differentiation. Each behavioral category entered the analysis in a stepwise mode, with $F=0.05$ to enter and $F=0.10$ to remove from the discriminating functions; the rule to select amongst available behavioral categories was to minimize Wilks' Lambda.

The behavioral sequences in each treatment group were transformed into a preceding–following acts transition matrix (one per group, per predatory phase). The significant cells (behavioral transitions; 5%, see Clark 1994) in these matrices were used to build the ethograms for the capture of each prey type.

To evaluate the whole predatory repertoire for each treatment group, we used the Directed Tree method (see Christofides 1975), as implemented in the software EthoSeq (Japyassú et al. 2006, available at http://www.assis.unesp.br/cats/ethoseq.htm). This method produces a hierarchical representation (DiTree) with all behavioral categories in the matrix placed as nodes in a branching diagram, whose base is called a root. Each matrix results in as many DiTrees as the number of behavioral categories included in it, each DiTree with a distinct category taken as its root. After selecting the root, the DiTree algorithm searches for the tree that maximizes the sum of the transition probabilities amongst all the behavioral categories, which means that the sequences therein are the most likely to occur given that root and data set. Each DiTree was decomposed in its branches, that is, the multiple linear sequences of behavioral categories from the root to each final leaf of the diagram. The linear sequences which occurred in the original videotaped data were called ‘behavioral routines’, and their incidence was compared among the treatment groups (for details, see Japyassú et al. 2006).

A Stereotypy Index (SI=number of individuals that executed the routine/total number of individuals) was computed for each of the behavioral routines detected via EthoSeq. This index varies from zero to one, and is higher for more stereotyped routines.

Comparative Analysis of the Predatory Repertoire

In order to understand the evolution of plastic responses, such as the predatory behavior, we made a survey of the literature about predation among spiders from the clade Orbiculariae, which comprises 15 spider families, Theridiidae included. There is considerable variation in the quality of data about predation published in the literature, due to differences in the main goal of each paper, as well as differences in sample size, number of prey species and other methodological details. To overcome these difficulties, we concentrated not on the whole predatory sequence, but rather on the attack tactic, because it has attracted considerable interest of arachnologists since the papers of Robinson (1969, 1975), and has thus been well documented in the literature.

Although some attack tactics are useful in phylogenetic analyses (see for example, the *bite*–wrap tactic—Griswold et al. 1998), we were interested in the plasticity of these tactics within each taxa. Thus, we did not concentrate on any particular tactic, but instead on the number of tactics displayed by each species, that is, on the size of the repertoire.

The resulting data was plotted on the phylogeny of the clade Orbiculariae (see Griswold et al. 1998), modified at the nodes subtending Tetragnathidae/Nephilidae (Hormiga et al. 1995; Kuntner 2006), Theridiidae (Agnarsson 2004) and Araneidae (Scharff and Coddington 1997), in order detail the relationships within each family. Some species were not present in any previous phylogenetic treatment, and in these cases we placed them basal to the other congeneric species, thus preserving the taxonomic information. Two of these species (*Comaroma simoni*, Anapidae, and *Mysmenopsis tengellacompa*, Mysmenidae) were the sole representatives of their families, and in this case, we simply placed them at their family node.

The attack repertoire was coded either as a two or three states character (nonadditive). In the first case, repertoires were coded as small (one to three attack tactics) or large (four to six); in the second case, repertoires were coded as small (one or two attack tactics), medium (three or four tactics), or large (five or six tactics). Repertoire size was optimized using the program Winclada (Nixon 1999–2002). Following a suggestion of de Pinna (1991), we preferred fast over slow optimization, because it preserves the primary homology statements.

The number of prey types[1] offered to each of the spider species varies from study to study, a situation that possibly introduces difficulties to the direct comparison of

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[1] We considered prey species of the same super-family taxonomic level as belonging to the same “prey-type” category. Prey from different developmental stages (i.e. adult vs larval beetles) were also considered different “types”.

the reported number of attack tactics, since the repertoire of some species can be better sampled than that of others. Since the size of the repertoire increases with the number of prey types offered to the spider (Japyassú and Viera 2002), for any of the species the reported number of attack tactics must be considered as an estimate of the real size of the attack repertoire. Thus, authors that studied predatory behavior using a small number of prey types (for example, Pasquet and Leborgne 1998; Harwood 1974, among others, see Table 2), could have underestimated the real size of the predatory repertoire in their study species. On the other hand, some authors have used a very large number of prey species (for example, Lubin 1980; Yoshida 1989).

In order to test the sensibility of the hypotheses of character evolution to these variations in the sampling of the attack repertoire, we have performed optimizations under two distinct scenarios, one with a weak and another with a strong "correction" on this sampling bias. Thus, we have changed the estimated number of attack tactics reported on Table 2 in two different ways. In the "weak correction" scenario, we lowered the number of attack tactics (for example, *Cyrtophora* species: number of tactics lowered from six to five) in the spider species whereupon the predatory repertoire was well sampled (that is, more than seven prey types offered in the study); conversely, we have raised the number of tactics (for example, *Araneus marmoreus*: number of tactics raised from two to three) in species considered to be poorly sampled (less than four prey types offered). In the second scenario, termed "strong correction", this scheme was maintained, except for species in the extreme of the sampling distribution (more than nine or less than two prey types offered); in these species we deleted or added two tactics from the repertoire reported in Table 2. Neither of these procedures were applied to *Mastophora dizzydeani* Eberhard 1980, because she is a predator known to be specialized on one sole prey type (moths, Eberhard 1980).

In one final attempt to deal with this same sampling bias problem, we have removed statistically variations in the size of the attack repertoire due to changes in sampling effort. We have removed the effects of the number of prey used in any particular study through a regression analysis (of the number of attack tactics over the number of prey types used in each study) and then traced the evolutionary history of the residuals of this regression. The fit of the data points to a linear regression model was tested through an ANOVA, and the significance of the model parameters was tested with the *t* Student statistic. We have performed the regression either with the raw data ($F_{(1,38)}=20.009$, $P<0.001$, $R=0.658$) or with the mean number of tactics per genera ($F_{(1,21)}=12.239$, $P=0.002$, $R=0.606$), always weighted by the number of prey. This second analysis was intended to reduce the effect of the phylogenetic correlation among data points in the estimate of the linear regression parameters, and weighting was used as a measure of support for each data point (Martins and Hansen 1996). Since the parameters of the adjusted line in the first analysis (parameter±SE: constant=1.104±0.439, slope=0.386±0.071) did not differ from the ones obtained in the second analysis (constant=1.089±0.570, slope=0.397±0.113), we plotted the standardized residuals of each species (first analysis) over the phylogeny using the software package Mesquite. The ancestral states for this continuous character were reconstructed with the parsimony method (squared parsimony model—Maddison and Maddison 2006). *M. dizzydeani* (a moth specialist, Eberhard 1980) was not included in this analysis; three other species [*Neriene radiata* (Walckenaer 1842), *Gasteracantha theisi* Guérin 1838 and *Gasteracantha taeniata* (Walckenaer 1842)] were also excluded, since we have no information concerning the number of prey offered to each of them (Eberhard 1967; Robinson and Lubin 1986).

Results

The spiders used a large predatory repertoire, one that was more diversified in the capture of beetle larvae. *A. digitus* showed a predatory behavior more stereotyped than that of orbweavers, although she presented both stereotypic—general patterns of predatory behavior—and variable aspects—plastic adjustments to local conditions—in her performance.

Analysis of Behavioral Stereotypy

The analysis with EthoSeq resulted in a large repertoire of 529 predatory routines. A large portion of this repertoire (44.42%) was independent of the context, that is, it occurred when both prey types were offered. Among these sequences were, for example, routines employed to temporarily store the prey at the periphery of the web. To do this the spider first immobilized the prey (wrap and *manipulate*), then she attached a thread to the web and moved up in the trap *paying out* a new line, which she attached to the retreat. Other routines were employed either in the capture of beetle larvae (30.25%) or in the capture of ants (25.33%).

The Stereotypy Index of the behavioral routines was similar for the captures of both prey types ($SI=0.11\pm0.12$, $U=176499.5$, $P=0.21$), but varied significantly among the capture phases ($F_{(2,37)}=27.16$, $P<0.001$). Detection was the most ($SI=0,14\pm0,04$), and immobilization the least ($SI=0,07\pm0,01$) stereotyped phase in the capture sequence (feeding phase: $SI=0,11\pm0,02$). A sample of the most stereotyped routines performed either to both prey types or to only one of them is presented in Table 1.

Predatory Patterns

The spider always oriented itself towards the prey by means of *tugging* movements (see Appendix 1 for detailed descriptions and discussions of the behavioral categories). Next, she *reeled* and wrapped the prey with viscid silk (sswrap). While wrapping with sticky silk the spider can either use alternate movements of leg IV (as when wrapping with dry silk) or, alternatively, she can use both legs simultaneously. In this case, she pulls the thread from the spinnerets with one leg IV; next the other leg IV stretches this new thread in the opposite direction and then both legs throw simultaneously the viscid line over the prey. The wrapped prey was left at the border of the retreat, suspended by a thread. The spider then turned and moved towards the prey and *manipulated* it; later she wrapped or bit the prey (Fig. 1a and b).

After biting the prey, the spider often returned to the retreat, just to search again for the prey, by means of *gropes*. Next the spider *retrieved* and *manipulated* the prey. In some cases, the spider attached a thread to the prey and carried it closer to the

Table 1 Most Stereotyped Routines (With Stereotypy Index—SI) Displayed in the Capture of Both Prey Types or Exclusively in the Capture of *Tenebrio* Larvae or Ants

Behavioral routine	*Tenebrio* larvae		Ant		SI
	Total	N	Total	N	
Tug/reel	16	16	14	14	0.75
Reel/wrap	12	12	13	13	0.625
Wrap/manipulate	71	16	33	15	0.775
Manipulate/bite	36	13	29	16	0.725
Wrap/fix	17	11	11	9	0.5
Pay out a line/fix and rotate/retrieve/manipulate	14	11	5	4	0.375
Fix and rotate/retrieve/manipulate	30	17	15	11	0.7
Wrap/carry/fix and rotate	13	11	4	4	0.375
Retrieve/manipulate/bite	13	9	13	12	0.525
Pay out a line/fix and rotate/pause/retrieve	5	5	–	–	0.125
Manipulate/wrap/carry on silk/fix and rotate/retrieve	5	5	–	–	0.125
Pay out a line/fix and rotate/pause/retrieve/manipulate	5	5	–	–	0.125
Fix and rotate/pause/retrieve/manipulate	6	6	–	–	0.15
Fix/pay out a line/fix	–	–	6	6	0.15
Groom/pause	–	–	9	7	0.175

"Total" is the total number of occurrences observed among the "*N*" spiders which displayed the routine. See Appendix for the definition of each behavioral category

retreat (sometimes the spider paid out a line instead of *carrying* the prey). Usually the predatory sequence ended with the spider in *pause* at the retreat.

Variations in Predatory Behavior

The detection phase of the capture of beetle larvae was more prone to mistakes in prey localization, causing the spider to *pause* and *tug* new gumfoot lines (Fig. 1a), a sequence that did not occur when preying upon ants (Fig. 1b). Furthermore, spiders engaged in the capture of beetle larvae often moved downward towards the prey while *reeling*; this was not the case in the capture of ants, in which the spider remained at the retreat while *reeling*. These differences resulted in a longer detection phase for the capture of beetle larvae, as compared to ants ($P=0.049$, $U=127000$, $N=40$).

Prey could be brought to the retreat by means of *reeling* or else could be transported hanging on the spinnerets. The first case was more frequent in the capture of ants and the second in the capture of beetle larvae. While capturing ants, the spider usually left the prey outside the retreat for a long time before returning to it.

The capture of beetle larvae could sometimes end with the spider *withdrawn* at the retreat, a condition that did not happen in the capture of ants (the spider usually finished the sequence with long *pauses* inside or even outside the retreat). Before ending the capture of ants the spider could groom her appendages, a behavior which was rarely observed in the capture of beetle larvae.

Although the whole capture of beetle larvae and ants had the same duration ($P=0.056$, $U=129{,}000$, $N=40$), they differed in the spider's level of activity. Spiders employed behavioral categories more frequently in the capture of beetle larvae ($P=0.005$, $U=98{,}500$, $N=40$). More specifically, the spider *tugged* (detection phase),

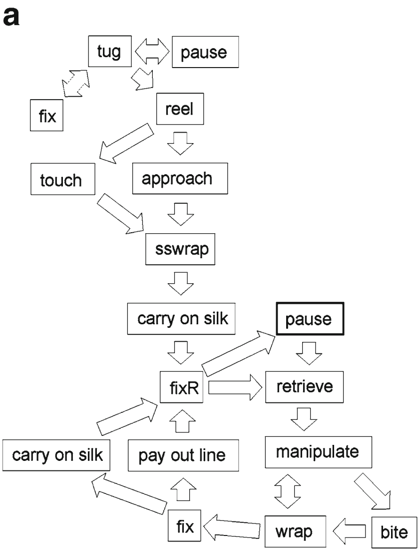

Fig. 1 Ethogram of the predatory behavior of *A. digitus*. **a** Spider preying on beetle larvae. **b** Spider preying on ants. *Continuous lines* represent significant transitions (5%, Clark 1994). *Dashed lines* represent most probable, non-significant transitions. Categories within a *bold box* are the most common endpoints of the predatory sequence. See the Appendix for the abbreviations and descriptions of behavioral categories. Rare behavioral categories (less than 1% of overall frequency) were not represented.

wrapped with sticky silk (immobilization), and left the prey at the border of the retreat (hanging on a thread, during the feeding phase) more frequently while capturing beetle larvae (discriminant analysis, $F_{(3,36)}=7.505$; $P<0.001$). Although these behaviors suffice to discriminate between the capture of both prey types, other behavioral categories were significantly and positively associated to them, hence occurring more frequently during the capture of beetle larvae (see Appendix). Only *grooming* was more frequent during the capture of ants.

Comparative Analysis

The number of attack tactics within the predatory repertoire varies among the species of the Orbiculariae clade (Table 2). In orbweavers such as Araneidae there is a large variation (from one to six attack tactics) and in derived araneoid sheetweavers, such as Theridiidae, this variation is reduced (from one to three distinct tactics).

We have plotted this information onto the phylogeny of the group, coding repertoire size as a character with either two or three states. In the three-states analysis, repertoire size is small at the base of Araneoidea, enlarges in a large clade within Araneidae (argiopines) and enlarges again within this same clade (*Cyrthophora* and *Argiope argentata*). The repertoire size also enlarges at the base of the nephilids (Fig. 2a).

In the two-states analysis, repertoire size is small at the base of Araneoidea and enlarges once within the argiopines, once within araneines (clades inside Araneidae), and once at nephilids (Fig. 2b). These analyses show that there is a basic

Table 2 Number of Attack Tactics of Spiders of the Orbiculariae Clade (Araneoids+Deinopoids)

Family	Species	Prey	Nprey types[b]	Ntactics[a]	tactics	References
Anapidae	*Comaroma simoni* Bertkau 1889	Collembolan, symphyle, onychiuridae	3	3	Bite–carry//bite–back off–carry (delayed carry)//bite	Kropf 1990
Araneidae	*Arachnura melanura* Simon 1867	*Drosophila sp* (Drosophilidae), nematocerans, moths, butterflies	4	3	Bite–wrap//wrap–bite//bite–pull out	Robinson and Lubin 1979
Araneidae	*Araneus marmoreus* Clerck 1757	Grasshopper, flies	2	2	Bite–wrap//wrap–bite	Pasquet and Leborgne 1998
Araneidae	*Araneus trifolium* (Hentz 1847)	Acridid Orthoptera, calyptrate Diptera, Lepidoptera	5	2	Bite–wrap//wrap–bite	Olive 1980
Araneidae	*Argiope amoena* L. Koch 1878	Crickets, moths, moth larvae, praying mantis, fireflies, flies	6	4	Bite–wrap//wrap–bite//wrap–carry–bite (delayed bite)//bite–pull out–carry–wrap (delayed wrap)	Hayakawa 1986
Araneidae	*Argiope argentata* (Fabricius 1775)	*Acheta domestica* (Gryllidae), moths, pentatomids, dragonflies, *Trigona* sp (Apidae), flies (*Musca domestica*), chrysomelids, acridid Orthoptera	8	5	Bite–wrap//wrap–bite//bite–pull out–wrap//out of web bite–wrap//bite–pull out–carry–wrap (delayed wrap)	Robinson 1969; Robinson and Olazarri 1971; Ades 1972
Araneidae	*Argiope aurantia* Lucas 1833	Orthoptera, Lepidoptera	2	3	Bite–wrap//wrap–bite//bite–pull out	Harwood 1974
Araneidae	*Argiope bruennichi* (Scopoli 1772)	Grasshoppers, crickets (Gryllidae), flies, moths, moth larvae, praying mantis, fireflies (Lampyridae)	7	4	Bite–wrap//wrap–bite//wrap–carry–bite (delayed bite)//bite–pull out–carry–wrap (delayed wrap)	Hayakawa 1986; Pasquet and Leborgne 1998
Araneidae	*Argiope ocyaloides* L. Koch 1871	Grasshoppers, calliphorid flies, moths	3	3	Bite–wrap//wrap–bite//bite–pull out	Robinson and Lubin 1979
Araneidae	*Argiope trifasciata* (Forskål 1775)	Acridid Orthoptera, calyptrate Diptera, Lepidoptera	3	2	Bite–wrap//wrap–bite	Olive 1980

Araneidae	*Cyrtophora citricola* (Forskål 1775)	Blowflies (Calliphoridae), fruitflies (*Drosophila* sp), stratiomyid flies, (moths, butterflies), katydids (Tettigoniidae), [Acrididae, Tetrigidae (grasshoppers)], dragonflies, pentatomid bugs, scarab beetles (Melolonthinae), weevils (Curculionidae)	10	6	Bite–wrap–cut out–free wrap//bite–pull out–wrap//bite–cut out–free wrap//wrap–bite–pull out//wrap–bite–cut out–free wrap//wrap–cut out–free wrap	Lubin 1980
Araneidae	*Cyrtophora cylindroides* (Walckenaer 1842)	Idem above	10	6	Bite–wrap–cut out–free wrap//bite–pull out–wrap//bite–cut out–free wrap//wrap–bite–pull out//wrap–bite–cut out–free wrap//wrap–cut out–free wrap	Lubin 1980
Araneidae	*Cyrtophora moluccensis* (Doleschall 1857)	Idem above	10	6	Bite–wrap–cut out–free wrap//bite–pull out–wrap//bite–cut out–free wrap//wrap–bite–pull out//wrap–bite–cut out–free wrap//wrap–cut out–free wrap	Lubin 1980
Araneidae	*Cyrtophora monulfi* Chrysanthus 1960	Idem above	10	6	Bite–wrap–cut out–free wrap//bite–pull out–wrap//bite–cut out–free wrap//wrap–bite–pull out//wrap–bite–cut out–free wrap//wrap–cut out–free wrap	Lubin 1980
Araneidae	*Eriophora fuliginea* (C.L. Koch 1838)	Crickets, moths, tenebrio beetles, *Trigona* sp	4	4	Bite–wrap//wrap–bite//bite–pull out//cut above–bite–wrap	Robinson, Robinson and Graney 1971
Araneidae	*Gasteracantha taeniata* (Walckenaer 1842)	A variety of insects[c]		1	Bite–wrap	Robinson and Lubin 1986
Araneidae	*Gasteracantha theisi* Guérin 1838	A variety of insects[c]		1	Bite–wrap	Robinson and Lubin 1986
Araneidae	*Mastophora dizzydeani* Eberhard 1980	Moths	1	1	Bite–wrap	Eberhard 1980
Araneidae	*Mecynogea lemniscata* (Walckenaer 1842)	*Musca domestica* (Muscidae), ant *Camponotus sayi*, asiatic oak weevils *Cyrtepistomus castaneus*	3	3	Bite–wrap//wrap–bite//wrap–carry–bite (delayed bite)	Willey et al. 1992

Table 2 (continued)

Family	Species	Prey	Nprey types[b]	Ntactics[a]	tactics	References
Araneidae	*Metazygia rogenhoferi* (Keyserling 1878)	*Atta* sp (Formicidae), *Tenebrio molitor* (Coleoptera), *Gryllus* sp (Gryllidae)	5	5	Bite–wrap//wrap–bite//bite–cut out–wrap//wrap–cut out–bite//cut above–wrap–bite?	Garcia, Cizauskas and Japyassú in prep
Araneidae	*Metepeira gressa* (Keyserling 1892)	Ant, *Musca* sp (Muscidae)	2	2	Bite–wrap//wrap–bite	Viera 1995
Deinopidae	*Deinopis longipes* F.O.P.-Cambridge 1902	Phasmid nymphs, beetles, ants, spiders, *Trigona* sp (Apidae)	5	1	Forward strike–wrap–bite	Robinson and Robinson 1971
Deinopidae	*Deinopis spinosa* Marx 1889	Moth, mosquito (Culicidae), tabanid, tipulid, *Drosophila* sp (Drosophilidae)	5	2	Forward and backward strike–wrap–bite	Coddington and Sobrevila 1987
Deinopidae	*Menneus camelus* Pocock 1902	Moth, spider	2	1	Forward strike–bite–wrap	Akerman 1926
Linyphiidae	*Neriene radiate* (Walckenaer 1842)	Live prey 1/3 the spider size	?[d]	2	Bite–wrap//bite–carry–wrap (delayed wrap)	Eberhard 1967
Mysmenidae	*Mysmenopsis tengellacompa* Platnick 1993	Ants, small insects	2	1	Bite–carry//bite–pull out–wrap (delayed wrap)	Eberhard et. al. 1993
Nephilidae	*Herennia ornatissima* (Doleschall 1859)	Moths, flies	2	2	Bite–wrap//bite–pull out	Robinson and Lubin 1979
Tetragnathidae	*Meta menardi* (Latreille 1804)	Diplopoda, Diptera, ants	3	4	Bite–wrap//wrap–bite//wrap–carry (delayed bite)//bite–pull out	Yoshida and Shinkai 1993
Tetragnathidae	*Meta reticuloides* Yaginuma 1958	Diptera, Hemiptera (stink bugs, leafhoppers), ants, bees, wasps, Lepidoptera, Orthoptera	8	3[e]	Bite–wrap//bite–pull out//wrap–bite	Yoshida 1990

Tetragnathidae	*Metleucauge kompirensis* (Bösenberg and Strand 1906)	Neuroptera, Orthoptera, Odonata, Plecoptera, Hymenoptera, Lepidoptera, Ephemeroptera, Diptera	8	2	Bite–wrap//bite–pull out	Yoshida 1989
Tetragnathidae	*Metleucauge yaginumai* Tanikawa 1992	Neuroptera, Orthoptera, Odonata, Plecoptera, Hymenoptera, Lepidoptera, Ephemeroptera, Diptera	8	2	Bite–wrap//bite–pull out	Yoshida 1989
Tetragnathidae	*Metleucauge yunohamensis* (Bösenberg and Strand 1906)	Neuroptera, Orthoptera, Odonata, Plecoptera, Hymenoptera, Lepidoptera, Ephemeroptera, Diptera	8	2	Bite–wrap//bite–pull out	Yoshida 1989
Nephilidae	*Nephila clavipes* (Linnaeus 1767)	Crickets (Gryllidae), moths, grasshoppers, tenebrio beetles (Tenebrionidae), *Trigona* sp (Apidae), pentatomids, blowflies	7	5	Bite–wrap//bite–pull out//bite–back off//long bite–pull out//cut above–bite–wrap	Robinson and Mirick 1971; Japyassú, Silveira and Oliveira in prep
Nephilidae	*Nephilengys cruentata* (Fabricius 1775)	Crickets (Gryllidae), flies, beetle larvae	3	5	Bite–wrap//bite–pull out//bite–back off//long bite–pull out//cut above–bite–wrap	Japyassú and Viera 2002; pers.obs.
Theridiidae	*Achaearanea cinnabarina* Levi 1963	*Tenebrio molitor* larvae (Tenebrionidae), ants	3	2	Sswrap–bite//sswrap–carry–bite (delayed bite)	Japyassú and Jotta 2005
Theridiidae	*Achaearanea digitus* Buckup et al. 2006	*Tenebrio molitor* larvae (Tenebrionidae), ants	3	2	Sswrap–bite//sswrap–carry–bite (delayed bite)	present paper
Theridiidae	*Achaearanea tepidariorum* (C.L. Koch 1841)	*Tenebrio molitor* larvae (Tenebrionidae), ants	3	2	Sswrap–bite//sswrap–carry–bite (delayed bite)	unpublished data
Theridiidae	*Argyrodes antipodianus* O. P.-Cambridge 1880	[*Drosophila melanogaster*, *D. immigrans* (Drosophilidae)], *Musca domestica* (Muscidae), [*Achaearanea* sp spiderlings (Theridiidae), *Araneus pustulosa* spiderlings (Araneidae)]	3	3	(Pull threads–vibrate–lunge)–bite–wrap//wrap–bite//pull threads–vibrate–lunge–bite	Whitehouse 1986

Table 2 (continued)

Family	Species	Prey	Nprey types[b]	Ntactics[a]	tactics	References
Theridiidae	*Argyrodes flavipes* Rainbow 1916	*Drosophila melanogaster* (Drosophilidae)	1	1	Wrap–bite	Whitehouse and Jackson 1998
Theridiidae	*Euryopis funebris* (Hentz 1850)	*Drosophila* sp (Drosophilidae), ants	2	1	Sswrap–bite	Carico 1978
Theridiidae	*Latrodectus geometricus* C.L. Koch 1841	*Tenebrio molitor* larvae (Tenebrionidae), ants	3	2	Sswrap–bite//sswrap–carry–bite (delayed bite)	Corrêa 2001
Theridiidae	*Theridion evexum* Keyserling 1884	*Tenebrio molitor* larvae (Tenebrionidae), ants	3	2	Sswrap–bite//sswrap–carry–bite (delayed bite)	Garcia and Japyassú 2005
Uloboridae	*Philoponella republicana* (Simon 1891)	*Drosophila* sp (Drosophilidae), [flies, mosquito (Culicidae)], flying ants, wasps, bees	5	1	Wrap–carry	Binford and Rypstra 1992

Only studies of predatory behavior that mention the prey taxa utilized are included in the table. Tactics of kleptoparasites (genus *Argyrodes*) were included only when employed towards active prey struggling on the web of the host. Although in the published papers we used only three prey types, we regularly feed these spiders in our lab with at least six prey types; in spite of that, we have not observed any tactic not described in the original papers

[a] Total number of attack tactics in each spider species

[b] Prey from the same superfamily were grouped [in brackets] in one single “type”, except for larvae and adults

[c] We considered this “variety” to be between four and seven prey types, in the two “correction” scenarios

[d] The authors do not provide this information. These species were not used in the two “correction” scenarios or in the analyses of residuals

[e] *Seize–pull out* was considered the same as *bite–pull out*, since most authors do not distinguish between seize and *bite*

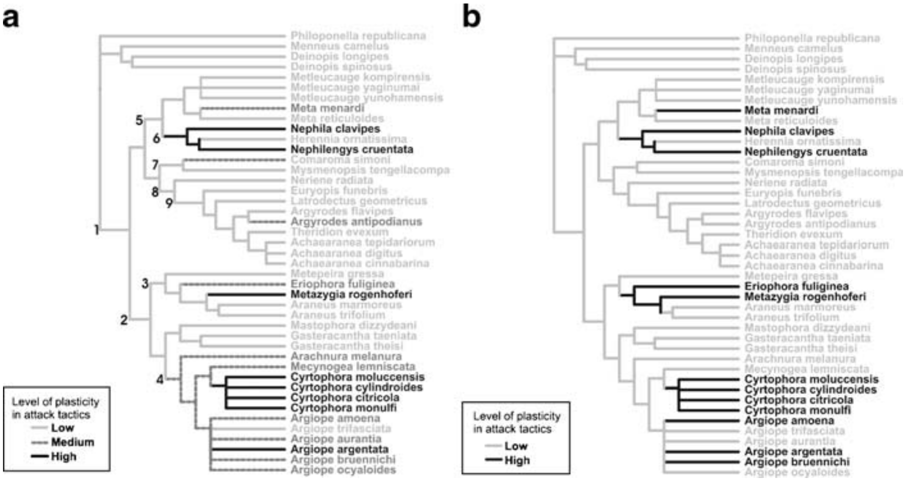

Fig. 2 Evolution of the size of the attack tactics repertoire (level of plasticity) among Orbiculariae. **a** Results with level of plasticity coded as a three-states character. **b** Results with level of plasticity coded as a two-states character. *Numbers* refer to clade names: *1* araneoidea, *2* Araneidae, *3* araneinae, *4* argiopinae, *5* Tetragnathidae plus Nephilidae, *6* Nephilidae, *7* symphytognatoidea, *8* araneoid sheetweavers and *9* Theridiidae.

evolutionary hypothesis which is not affected by the coding scheme: the attack tactics repertoire evolves independently two times from an ancestral small size to a larger one (within the families Nephilidae and Araneidae, Fig. 2).

In order to test the sensibility of this evolutionary hypothesis to possible bias in repertoire size estimation, we have also plotted a “corrected” repertoire size onto the phylogeny of the group. Both strong and weak correction scenarios resulted in minor optimization changes.

Weak correction. Three states: repertoire size is small at the base of araneoidea, enlarges at Nephilidae and within Araneidae; in this last case, it enlarges once at the base of the family and once more at the *Cyrtophora* clade (Fig. 3a). Two states: repertoire size is small at the base of Araneoidea and enlarges at Nephilidae and within Araneidae (within araneines and argiopines).

Strong correction. Three states: repertoire size is small at the base of araneoidea and enlarges at Nephilidae and Araneidae (Fig. 3b). Two states: repertoire size is small at the base of araneoidea and enlarges at Nephilidae and within Araneidae (araneines and argiopines).

In a last attempt to deal with the effect of the differential repertoire size sampling effort among the diverse studies herein reviewed (Table 2), we have estimated the ancestral states of the standardized residuals of the weighted regression between attack repertoire size and number of prey types (squared length of the reconstruction: 22.2949). Thus, the residuals in this analysis are the portion of repertoire size that is not explained by the number of prey types. The most parsimonious ancestral states for the residuals (reconstructed through the “trace” menu of the program Mesquite, using parsimony of ancestral states, with the Squared parsimony model), are low at the base of araneoids (−0.38—clade 1 at Fig. 2a). Ancestral states are low at all the nodes leading to Nephilidae (node subtending all araneoids except Araneidae: −0.34;

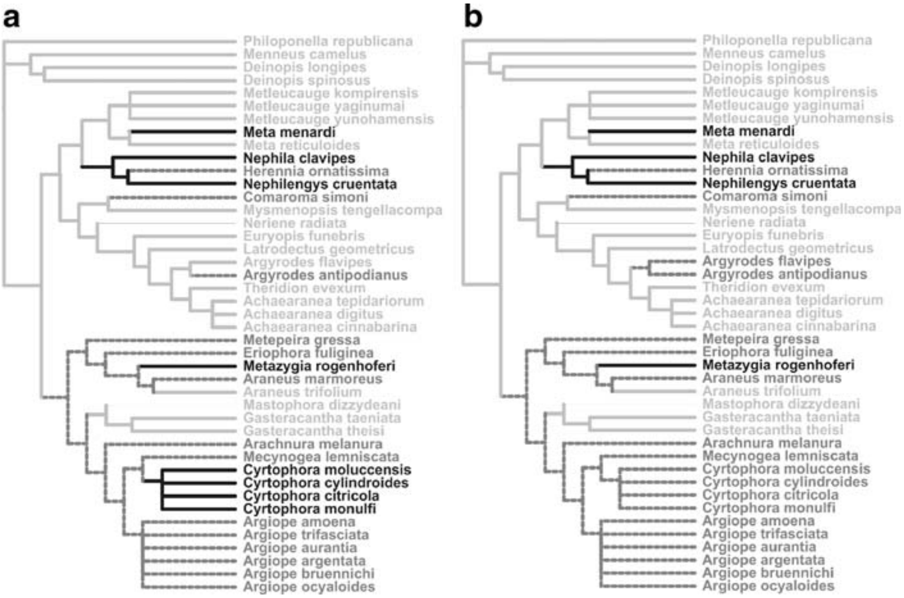

Fig. 3 Evolution of the size of the attack tactics repertoire (level of plasticity) among Orbiculariae, with corrections for sampling bias. **a** Weak correction scenario and **b** strong correction scenario. Data for *Neriene radiata* is ambiguous, since we have no information concerning the number of prey types for this spider; also, *Mastophora dizzydeani* was excluded from these analyses (see text). Legend the same as in Fig. 2a.

symphytognatoidea+araneoid sheetweavers: −0.33; Nephilidae+Tetragnathidae: −0.32). The ancestral states are positive only for Nephilidae and Araneidae. They increase strongly at the base of these two groups (Nephilidae: from −0.32 to +0.68; Araneidae: from −0.36 to +0.11), and they further increase within Araneidae (to +0.37 among araneines, clade 3 at Fig. 2a, and to +0.33 among argiopines, clade 4 at Fig. 2a). Finally, this analysis show an unexpected decrease in the residuals at the node subtending *Metleucauge*+*Meta* (from −0.32 to −0.80). Thus, this analysis confirms the results from the previous analyses. The repertoire size (the portion not explained by the number of prey types) is small at the base of araneoidea and enlarges at both Nephilidae and Araneidae.

Discussion

The predatory repertoire of *A. digitus* is largely stereotyped and this high level of stereotypy is a plesiomorphic characteristic of the family (Theridiidae). Theridiids seem to have remained with a small repertoire of attack tactics due to the evolution of a special wrapping technique. This predatory stereotypy contrasts with the plasticity in other aspects of foraging behavior (web building and design). We will argue that this contradiction is only apparent, since in both cases the important point is that there is a simplification in the mechanisms underlying behavioral expression.

Stereotypy Among Araneoid Sheetweavers

A large portion of the predatory repertoire of *A. digitus* is stereotyped, that is, displayed in the same way in distinct contexts. More than one third of its behavioral routines (44.42%) were employed in the capture of both beetle larvae and ants. This is also true for other species in the same family (studied within the same experimental setting used in the present paper), such as *Theridion evexum* Keyserling 1884 (47,3%—Garcia and Japyassú 2005), *Achaearanea cinnabarina* Levi 1962 (35.4%—Japyassú and Jotta 2005), *Latrodectus geometricus* Koch 1841 (39,8%—Corrêa 2001) and *Achaearanea tepidariorum* (Koch 1841) (41.7%—unpublished data). This high level of stereotypy among araneoid sheetweavers contrasts with low levels for orbweavers studied in similar settings, such as *Nephilengys cruentata* (Fabricius 1775) (Nephilidae; 19.47%; Japyassú and Viera 2002). Thus, the foraging behavior of araneoid sheetweavers is less adjustable to local conditions than that of orbweavers, a result that seems to contradict previous reports (Eberhard 1990, 2000; Benjamin and Zschokke 2004, but see discussion below).

Another evidence pointing in this same direction comes from the evolution of attack tactics in the Orbiculariae clade. Low number of tactics means reduced possibilities of adjusting behavior to variable conditions (such as variable prey types), that is, high stereotypy. The number of attack tactics increases independently within two orbweaver families (nephilids and araneids), but is kept low throughout the evolution of the araneoid sheetweavers (Fig. 2a). High predatory stereotypy is a plesiomorphic trait in the whole group, one from which plasticity evolves independently at least two times.

Among the most stereotyped routines of *A. digitus* are the ones involved in prey localization, such as *tug/fix/tug* followed by *tug/reel*, employed to both prey types. These sequences are mainly a byproduct of the structure of the web. The prey is entangled to the viscid basal tip of gumfoot lines, which are connected to the upper retreat where the spider rests. The spider thus must *tug* successive gumfoot lines before striking to the one bearing the prey. This also occurs among other theridiids, such as *T. evexum*, *A. cinnabarina*, *L. geometricus* and *A. tepidariorum* (Garcia and Japyassú 2005; Japyassú and Jotta 2005; Corrêa 2001) and is probably a trait present in all gumfoot web building spiders, since it is present even among the distant and unrelated pholcids (Japyassú and Macagnan 2004).

Biting the prey after *wrapping* it with sticky silk (*sswrap/manipulate/bite*) is another stereotyped sequence, used mainly against ants in *A. digitus*. While *wrapping* with sticky silk the spider can either use alternate movements of leg IV (as when *wrapping* with dry silk) or, alternatively, she can use both legs simultaneously. In this case, she pulls the thread from the spinnerets with one leg IV; next the other leg IV stretches this new thread in the opposite direction and then both legs throw simultaneously the viscid line over the prey. This special way of wrapping was also described for *A. cinnabarina* (Japyassú and Jotta 2005), and Eberhard (1979) shows a picture where *Argyrodes attenuatus* seems to use simultaneously both legs while throwing viscid silk onto the prey.

Other theridiids also subdue their prey with *sswrap–bite* (Coddington 1986), although it is not known whether they use the special technique described above.

Sswrap/bite is a routine that postpones the contact with the prey, and *A. digitus* sometimes postpones even more this contact, with variant tactics such as *sswrap/fix/pay out a line/fix and rotate/retrieve/manipulate/bite* (see Table 1). Orbweavers can employ other tactics, such as *bite*/transport or *bite/wrap* (Ades 1972), and these tactics involve a quick and direct contact with the struggling prey. Postponing contact can be important when dealing with potentially aggressive prey, and this is exactly the case in theridiids, which include in their diet a large proportion of ants (up to 75% of their diet—Holldobler 1970; Carico 1978; MacKay 1982; Nyffeler and Benz 1987; Nyffeler et al. 1988; Breene et al. 1989, 1993; Nyffeler 1999). Thus it seems to us that theridiid predatory tactics have remained uniform because they have evolved a technique which involves the direct use of sticky lines applied through the use of simultaneous movements of legs IV. If the spider uses both legs to throw the viscid thread during the first contact with prey, it enhances the chances of hitting its somewhat mobile target, for it covers an area which can be as large as the distance between the tips of its fourth legs. *Sswrap* is efficient in the capture of all prey types, even the dangerous ones, thus precluding the need of specialized techniques for distinct prey types. This tactic probably evolved from the Orbiculariae *wrap–bite* tactic, which could have been modified through the addition of glue to the wrapping silk, and through the simultaneous use of legs IV.

Evolution of Predatory Plasticity

The analyses of repertoire size evolution show striking similar results. Repertoire evolves independently from a small to a large size within two orbweaver families: Nephilidae and Araneidae. This hypothesis appeared in all the meta-analyses we performed: it proved robust enough to resist sampling bias corrections under two character coding schemes (two or three states); it also proved correct when the effect of sampling bias was statistically removed[2].

Departing from a basal repertoire including *bite/pull out* (to small prey) and *bite/wrap* (to large but harmless prey, see Eberhard 1982 and Robinson 1975), spiders in the nephilid lineage have added to their attack repertoire tactics such as *bite/back off* (Robinson and Mirick 1971; Robinson and Robinson 1973), and *cut above/bite/wrap* (cut the web just above the prey and proceed to the *bite/wrap* sequence—Japyassú and Viera 2002), whenever preying upon large and potentially aggressive prey.

Within araneids, increases in plasticity occur with the addition of the tactic *wrap/carry/bite* (for example, in *Mecynogea*, *Argiope*), and of many new tactics in *Cyrtophora* species, such as *wrap/bite/pull out*, *wrap/bite/cut out/free wrap* or *bite/wrap/cut* out/*free wrap*. These synapomorphies were built upon a plesiomorphic repertoire including *bite/pull out* (Robinson 1975), *bite/wrap* (Scharff and Coddington 1997) and possibly *wrap/bite* (Coddington 1989, but see Scharff and Coddington 1997). The evolution of *wrap–bite* is somewhat controversial. Eberhard (1967) argued that *wrap–bite* probably evolved from wrapping at the feeding site (*bite/wrap*), Robinson et al. (1969) supported this general hypothesis from within the

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[2] While the present paper was *in press*, Kuntner et al. (2007) suggested an alternative phylogenetic position to the family Nephilidae, but this alternative phylogeny does not alter the hypothesis here discussed.

family Araneidae, and Robinson (1975) added weight to these views based on data from Nephilidae and Araneidae. Coddington (1989, p.90) disagreed, suggesting that immobilization wrapping was plesiomorphic for all orbweavers, and that its use was reduced in derived araneoids (i.e., Tetragnathidae, Nephilidae, Anapidae, Theridiosomatidae, Mysmenidae, Theridiidae, Nesticidae and Linyphiidae). Nevertheless, studying a larger dataset within an explicitly phylogenetic framework, Scharff and Coddington (1997) agreed with the earlier views, adding that *wrap–bite* must have evolved independently many times from the plesiomorphic *bite–wrap*.

Plasticity Evolution and Environmental Heterogeneity

It has been argued that the evolution of phenotypic plasticity is favored by environmental heterogeneity or unpredictability (see for example Zhivotovsky et al. 1996; Schlichting and Pigliucci 1998; West-Eberhard 2003) and, the other way round, that phenotypic stereotypy is favored by environmental homogeneity (or predictability). We argue that this is not the case, or at least that this “predictability-stereotypy” hypothesis cannot explain the evolution of foraging plasticity among araneoid spiders. Instead, we propose that higher environmental predictability is associated not to behavioral stereotypy, but rather to simplicity of the underlying information processing mechanisms.

If environmental predictability selects for behavioral stereotypy, then foraging among araneoid sheetweavers should be more stereotyped than among orbweavers. This is because araneoid sheetweavers are exposed to less variable environments than do orbweavers. In a comparative study of spiders from these two guilds, Janetos (1982) found that araneoid sheetweavers’ web-sites have less variable payoffs than do the web-sites of orbweavers; Janetos found that araneoid sheetweavers face smaller variability not only in the number of prey items captured per day, but also in the size of these prey items. Araneoid sheetweavers also have higher web-site tenacity than do orbweavers (Janetos 1982), and this is probably a consequence of the high cost of sheetwebs in general, since Janetos (1986) and Riechert and Gillespie (1986) show this same tendency even when comparing non-araneoid sheetweavers with orbweavers. Staying longer at a web-site means to be exposed to a lower lifetime number of web-sites, and their surrounding influences. If we sum to this the lower prey variability that araneoid sheetweavers face, it seems that each individual is exposed to less variable environments, a situation that should in the long run select for higher stereotypy. Nevertheless, araneoid sheetweavers have evolved contradictory tendencies: plasticity in one aspect of foraging behavior (web building and design, Benjamin and Zschokke 2004; Eberhard et al. 2008) and stereotypy in another aspect of this same behavior (predatory sequence, present paper), a result that is not in accord with the predictability-stereotypy hypothesis.

In order to account for these results we put forward a modified hypothesis: predictability or homogeneity of environmental features should select not exactly for behavioral stereotypy, but for simplicity of the underlying information processing mechanisms controlling behavioral expression. The less complex the habitat, the less complex the neural circuitry required to survive on it. The point is that neither simplicity in neural circuitry implies stereotyped behaviors, nor complexity of this circuitry necessarily entails plastic behaviors. For example, in the present paper we have shown increases in araneoid foraging plasticity obtained by diverse ways of adding new routines to a plesiomorphic repertoire, all of which require an increase in the complexity of the underlying information processing system. This is because these spiders must not only include new or modified behavioral categories into their activity repertoire (i.e., must have new neural circuitry for these new motor actions), but also, at the perceptual level, they must add neural circuitries for the discrimination between distinct kinds of prey, and also neural connections that allow this discrimination to lead to decisions of the kind: if prey “a”, then tactic “A”, if prey “b”, then tactic “B”. Increases in behavioral plasticity due to increases in neural circuitry are well documented, for example, among song learning birds (Brenowitz 2004). Nevertheless, plasticity increases have also been obtained through reductions on the information processing mechanisms. Plasticity in behavioral expression can be the result of inherent imprecision in neural control (Eberhard 1990, 2000), or else be the result of the loss of organized behavioral units (or whole cycles of interaction between these units, such as phases in web building among araneoid sheetweavers—Benjamin and Zschokke 2004; Eberhard et al. 2008), and in either case it is coupled with lowered levels of information processing mechanisms.

If this predictability-simplicity hypothesis is correct, we expect to find examples, other then the above detailed, of less variable evolutionary environments leading to more plastic phenotypes. This is because, in this modified hypothesis, environmental predictability selects for a simplification of the information processing system underlying behavioral expression, a simplification that can result on either stereotyped or plastic behaviors.

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Appendix

Behavioral categories employed in the description of capture sequences

Category names are in *italics*. Categories followed by a symbol are significantly and positively associated to *fixR* (•), *tug* (✟), or *wrap* (*), the three categories which most contribute to the differentiation between the capture of beetle larvae and ants.

Approach: spider displacements towards the prey, without tensing the threads with the first pair of legs (see *tug* bellow). It occurs during the detection phase and is usually followed by prey-touching or prey-wrapping movements. Viera (1986) describes a similar category, “desplazamiento 2”, but her description encompasses both *approaching* and *tugging* movements.

Bite • (Robinson and Olazarri 1971): the spider extends the distal segments of the chelicerae and flexes one segment against the other onto the prey, touching or penetrating it for a long time. Viera (1986) divides the observed *bites* for *Metepeira* sp. in long, sustained insertions (during at least 20 s) and short, subtle insertions of chelicerae onto prey. In this paper we did not consider this distinction.

Carry on silk * (Robinson and Olazarri 1971): after the spider attached a thread onto the wrapped prey, she moves toward the retreat, *carrying* the prey behind it, held by the spinnerets or by one of the posterior legs (leg IV). Robinson and Mirick 1971 (see also Robinson and Olazarri 1971, Robinson and Robinson 1973) describe another category, *carry on jaws*, carried out by large spiders usually when preying upon small prey items; this category does not seem to occur among theridiids.

Cut thread (Robinson and Olazarri 1971): the spider cuts the threads either with her legs or chelicerae. She can cut the lines enveloping the prey, the lines connecting the prey to the web or the web lines.

Fix •*✟ (Viera 1994): the spider moves her abdomen ventrally, touching the web or prey with the spinnerets, attaches a thread and leaves a new silk strand.

Fix and rotate (*fixR*; Robinson and Olazarri 1971; Viera 1994): after attaching the wrapped prey to the retreat, the spider turns to assume a head-down posture. During the turning process, the spinnerets are dabbed against the web in an arc. This sequence of web fixations during the turning process is named *fixR*. Peters (1931, apud Robinson and Olazarri 1971) describes this same movement (which he called *Rundgang*) for *Araneus diadematus* Clerk 1757.

Grooming (Robinson and Olazarri 1971): the spider rubs the appendages one against the other or against the spinnerets and/or abdomen. She also makes chewing movements with the chelicerae while passing slowly the tarsi of the appendages, one by one, between the chelicerae. She can also rub one chelicerae against the other.

Grope: at the retreat, the spider searches for the prey that is packed, hanging nearby on a thread. She tenses some of the web threads with legs I before she moves in the right direction (see *retrieve* below). This tensing looks like a *tugging* (see below), but is more subtle and occurs only after prey immobilization.

Manipulate •* (Robinson and Olazarri 1971): repeated touches on the body of the prey, with palps, legs or chelicerae, turning the prey package around and delivering short *bites* at various regions. In the present paper we excluded these short *bites* from manipulation.

Pause ✟ (Viera 1994): the spider halts at any moment of capture sequence and stands immobile (not *withdrawn*, see below) during 30 s or more.

Pay out a line • (Japyassú and Macagnan 2004, Garcia and Japyassú 2005): the spider attaches a thread to or nearby the wrapped prey and moves towards the retreat, leaving behind a dragline. As a variation of this category, the spider can stop a *wrapping* bout and move towards the retreat, leaving a new dragline without previously attaching the thread to the prey.

Reel (Japyassú and Macagnan 2004, Garcia and Japyassú 2005): usually at the retreat, the spider pulls the gumfoot line with her front legs (legs I, occasionally also with legs II), thus bringing the prey adhered to the gumfoot bellow towards herself. The spider first extends one leg I, grabs the gumfoot line and flexes the leg. She then alternates these same movements with both legs I, thus bringing the prey towards herself. The spider can occasionally extend and/or flex both legs at the same time. Ades (1972) describes a similar behavior (*lifting*, also named *retrieve* by Japyassú and Viera 2002). Although topologically similar, these behaviors occur in completely different contexts: *reeling* occurs before the contact with prey, during the detection phase, and *lifting* occurs long after prey immobilization, when the spider is at the retreat or hub and the prey is packed, hanging on a nearby thread.

Retrieve • (Japyassú and Macagnan 2004, Garcia and Japyassú 2005): usually at the retreat, the spider moves towards the wrapped prey that is hanging nearby on a thread or entangled at the periphery of the web. Viera (1994) describes a similar category (*recuperación*), but in this description the spider pulls the wrapped package towards her using legs I and II, instead of moving towards the prey. Although the result is the same (the spider touches the prey), the topology of the movement is very distinct. *Retrieve* is very usual and widespread among theridiids, but is rare among orbweavers.

Return •✟: the spider moves towards the retreat without leaving a dragline behind. This can occur before a sticky silk *wrapping* bout (see *wrap* below), usually when the spider fails to hit the prey.

Tug (Jackson and Brassington 1987): at the retreat, the spider moves legs I medially, while grasping silk lines with the leg tarsi. She holds the lines tensed for 1–2 s then relaxes its legs, returning to the normal position. The spider usually moves towards the prey before tensing the threads with legs I. She also *tugs* consecutively nearby gumfoot lines before *reeling* (see *reel* above) one of them.

Withdraw (Lubin 1980): Lubin observed this behavior in four species of *Cyrtophora*. She describes it as a cryptic position that involves pulling all the legs inward towards the body, thereby obscuring the typical spider-like outline.

Wrap (Robinson and Olazarri 1971): after *reeling* the prey, or after *approaching* and/or *touching* it, the spider throws dry (*wrap*) or viscid (*sswrap*) silk onto it, with alternate movements of legs IV, which repeatedly touch the spinnerets and move towards the prey. While legs IV cast silk, legs III hold the prey and the other legs hold web lines. The topology of these movements in *A. digitus* is similar to the one described for the orbweavers of the family Araneidae, and even for the unrelated spiders of the family Pholcidae (see Jackson and Brassington 1987, Japyassú and Macagnan 2004), but it is strikingly different from the one observed for *Euryopis funebris* (Hentz 1850), another theridiid (see Carico 1978). In an alternative, special wrapping technique, *sswrap* can be iniciated with simultaneous movements of legs IV, from the spinnerets to the prey: the spider first takes a thread (coated with viscid blobs) with the tip of one leg IV and then extends this leg laterally; next she grips this same line with the other leg IV and, with both legs, throws over the prey the viscid segment that is between her legs (Japyassú and Jotta 2005); these movements are repeated many times in a single *wrapping* bout. We have not observed the "bobbin like" wrapping that Robinson and Olazarri described for *Argiope argentata* (Fabricius 1775).

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