

Homology in a context dependent predatory behavior in spiders (Araneae)

Vanessa Penna-Gonçalves: Laboratório de Artrópodes, Instituto Butantan, Avenida Vital Brazil 1500, São Paulo SP, 05503-900, Brazil; Departamento de Psicologia Experimental, Instituto de Psicologia, Universidade de São Paulo, Brazil

Carolina Ribeiro Martins Garcia: Laboratório de Artrópodes, Instituto Butantan, Avenida Vital Brazil 1500, São Paulo SP, 05503-900, Brazil

Hilton Ferreira Japyassú¹: Laboratório de Artrópodes, Instituto Butantan, Avenida Vital Brazil 1500, São Paulo SP, 05503-900, Brazil

Abstract. Stereotyped behaviors have been routinely used as characters for phylogeny inference, but the same cannot be said of the plastic aspects of performance, which routinely are taken as a result of ecological processes. In this paper we examine the evolution of one of these plastic behavioral phenotypes, thus fostering a bridge between ecological and evolutionary processes. Foraging behavior in spiders is context dependent in many aspects, since it varies with prey type and size, spider nutritional and developmental state, previous experience and, in webweavers, is dependent on the structure of the web. Reeling is a predatory tactic typical of cobweb weavers (Theridiidae), in which the spider moves the prey toward her by pulling the capture thread (gumfoot) to which it is adhered. Predatory reeling is dependent on the gumfoot for its expression, and has not been previously reported in orbweavers. In order to investigate the evolution of this web dependent behavior, we built artificial, pseudogumfoot lines in orbwebs and registered parameters of the predatory tactics in this modified web. Aspects of the predatory tactics of 240 individuals (12 species in 4 families) were measured, and the resulting data were optimized on the phylogeny of Orbiculariae. All species perform predatory reeling with the pseudogumfoot lines. Thus, predatory reeling is homologous for the whole Orbiculariae group. In nature, holes made by insects in cribellate orbs produce pseudogumfoot lines (similar to our experimentally modified webs), and thus reeling occurred naturally in cribellates. Nevertheless, outside lab conditions, predatory reeling does not occur among cribellate orbweavers, so that this behavior could not have been selected for in the cribellate ancestor of orbweavers. Cribellate spiders are flexible enough as to present novel and adaptive predatory responses (reeling) even when exposed for the first time to conditions outside their usual environment. Thus, the evolution of reeling suggests an alternative mechanism for the production of evolutionary novelties; that is, the exploration of unusual ecological conditions and of the regular effects these abnormal conditions have on phenotype expression.

Keywords: Behavior, evolution, orbweb, gumfoot, predatory sequence

Although stereotyped behaviors have been routinely used as a basis for phylogenetic inference in spider literature (Eberhard 1982; Coddington 1986; Griswold et al. 1998; Kuntner et al. 2007), the same is not true of the plastic aspects of performance, those dependent on context for their expression. Plasticity refers to learning (Pigliucci 2001) or, more generally, to aspects of performance that vary with the context of its occurrence, such as variability of the predatory sequence as a function of the kind and size of prey (Robinson 1975; Li 2000; Garcia & Japyassú 2005), or variability in web parameters as a function of the presence of specific prey (Sandoval 1994) or the presence of predators (Li & Lee 2004). The logic underlying the use of stereotyped behaviors for phylogeny estimation is the same as that underlying the use of morphological data: stereotyped behaviors are as species typical as morphology, and it has been shown that there is no significant difference between those two kinds of data in assessing phylogeny (de Queiroz & Wimberger 1993). Although the same may not be true of the plastic aspects of performance, because of its closer connection to environmental factors, even these plastic aspects of behavior can be subjected to selection (Daly et al. 1982). These more complex behavioral phenomena could reveal details of a more intricate evolutionary process, one with simultaneous competing

selection pressures, besides providing a richer database for extracting phylogenetic patterns (Japyassú & Viera 2002). Also, the ability to make plastic adjustments varies among taxonomic groups and this ability could itself provide useful characters for phylogenetic analyses (Japyassú & Caires 2008).

As an example of the evolutionary intricacies that context dependency can unravel, we focus here on the evolution of a putative behavioral synapomorphy of cobweb spiders (Theridiidae): a typical attack tactic named reeling. Most theridiid webs have gumfoot lines or lines with glue droplets spread all over (Benjamin & Zschokke 2003). These special capture threads extend from a structural net (where the spider rests) to the substrate. Prey items adhere to the gumfoot, and then the spider walks under its sheet/net to touch this capture line, which it reels in with alternate movements of its front legs (while legs III roll up the capture line producing a silken pellet), bringing the prey close enough to be wrapped with viscid silk. If the prey has escaped from the gumfoot and is walking nearby, the spider can walk down the gumfoot and leave the web, walking over the ground searching for the prey (Japyassú & Jotta 2005; Garcia & Japyassú 2005).

Reeling and the other behaviors related to gumfoot lines (such as the above described sticky silk wrapping and ground search, as well as gumfoot line building) have also been observed in a phylogenetically distant family (Pholcidae, Japyassú & Macagnan 2004). The homoplasious co-occur-

¹ Corresponding author. E-mail: Japyassu@butantan.gov.br

rence of this potentially independent set of behaviors suggests that they somehow require one another, that together they form a complex adaptation. Since these behaviors are all related to a single web structure, the gumfoot, it is tempting to think that gumfoot evolution could facilitate the appearance of the other associated behaviors, that gumfoot lines could somehow function as a stimulus to the occurrence of those units of predatory behavior. Predatory behavior is overtly context dependent (Robinson & Olazarri 1971; Coddington & Sobrevila 1987; Edwards & Jackson 1993, 1994; Jackson & Wilcox 1993; Jackson & Pollard 1996; Japyassú & Viera 2002; Japyassú & Jotta 2005), and the web is the most immediate context for its expression. So, it is not unreasonable to suppose that the evolutionary appearance of web structures (gumfoot lines) could lead to abrupt changes in web-based behaviors. In the present paper we comparatively explore this possibility, experimentally manipulating the context (web) of predatory performance in a number of spider families related to cobweb weavers (Theridiidae). Since the Orbiculariae outgroups of theridioids (Theridiidae + Nesticidae), namely linyphioids (Linyphiidae + Pimoidae) and orbweavers, do not build gumfoot lines (Benjamin & Zschokke 2003, 2004), we have created “gumfoots” in the orbwebs in order to register possible new predatory behaviors occurring in this new, artificial web context.

We use this experimental, comparative data, to understand the evolution of a context dependent behavior (predatory reeling), plotting its occurrence (in this modified web context) on the phylogeny of the group. We also discuss the implications of these results for the evolution of context dependent behaviors in general.

METHODS

Artificial gumfoot lines (pseudogumfoot lines) were produced in orbwebs (see below), and the predatory behavior on these modified webs was compared to that performed on naturally gumfooted theridiid webs. Spider species were chosen for their abundance, phylogenetic position, and possibility of web manipulation. Twelve species distributed in four families were included in the analysis, each comprising 20 adult females (each spider was observed for only one predatory sequence). The orbweavers *Zosis geniculata* (Olivier 1789) (Uloboridae), *Micrathena nigrichelis* Strand 1908, *Alpaida veniliae* (Keyserling 1865), *Metazygia rogenhoferi* (Keyserling 1878), *Metazygia gregalis* (O. Pickard-Cambridge 1889) (Araneidae), and two unidentified *Leucauge* species (Tetragnathidae) were observed in this study. Information about five species of cobweavers (Theridiidae) was extracted from previous studies in the lab (see below). Spiders were collected at various remnants of Atlantic forests in São Paulo city (Brazil): reserve of the São Paulo University (“Armando Salles Oliveira”, CUASO, 23°33'S, 46°43'W), Morro Grande reserve (Cotia, 23°40'60"S, 47°01'60"W), Ilha dos Eucaliptos (island in Guarapiranga reservoir, 23°43'59.90"S, 46°44'02.53"W), Parelheiros (area on the edge of the Guarapiranga reservoir, 23°43'58.86"S, 46°44'27.27"W), Guarapiranga Park (23°40'28.54"S, 46°43'55.39"W) and Oswaldo Cruz Park (Instituto Butantan, 23°33'S, 46°43'W). Voucher specimens were deposited in the arachnological collection at Instituto Butantan (IB57626–46, IB57434–42, IB57392–99 e IB 57560–88; curator A.D. Brescovit).

For each specimen, we observed the predatory behavior until the first contact with the prey (*Gryllus* sp. of the same size as the spider — cephalothorax + abdomen). We measured the displacement (cm) of the spider and/or of the prey (through reeling) in the gumfoot (or pseudogumfoot) for each specimen and expressed this measure as a percent of the total capture thread length [reeling extent (RE)]. We considered that the spider reeled if the prey was displaced as a result of alternate movements of the front legs pulling the capture line.

The spider predatory behavior was separated into two categories: definite or mixed responses. In definite responses the spider could either entirely reel in the (pseudo)gumfoot (i.e., standing at the hub, the spider pulled in the entire gumfoot line with her front legs, until she touched the prey, RE = 100) or she could not reel it in at all, walking from the hub to the prey along the capture line (RE = 0). In the mixed responses the spiders first walked along the length of the capture line and then initiated reeling movements ($0 < RE < 100$).

Web context manipulation.—Pseudogumfoot lines were produced in the orbwebs of spiders from three families (Uloboridae, Araneidae, and Tetragnathidae). For our purposes, the main difference between a real gumfoot line in a cobweb and a radius in an orbweb is that the gumfoot is easily detached from its point of attachment on the substrate (through reeling), while the radius is firmly attached to the frame of the orb (forbidding the execution of reeling). Thus, in order to make a radius more similar to a gumfoot, we simply cut it at the midpoint from the hub to the frame. This loose radius was called a pseudogumfoot. The prey was then left at the free end of this pseudogumfoot (Fig. 1a). The radius selected for this procedure was always in the lower portion of the webs, in the middle of an intact sector of the orb.

This procedure was modified in the web of the cribellate *Z. geniculata*. The adhesive spiral in cribellate webs is less extensible than in the ecribellate ones (Kölher & Vollrath 1995). Thus, even with a free end, the cut radius (pseudogumfoot) was still firmly connected to the rest of the trap through a bunch of poorly extensible, cribellate adhesive spiral threads that prevented reeling. In order to overcome this difficulty, we freed this radius even more, also cutting all the adhesive spiral threads except for the most peripheral one (Fig. 1b).

We have not succeeded in producing similar pseudogumfoot lines in the web of the linyphiid *Dubiaranea* sp., because her trap is composed of a horizontal sheet of densely interwoven threads with nothing similar to radii or spirals. We have tried to make *Dubiaranea* sp. specimens adopt the web of other species (for example, theridiid webs), but again we did not succeed. As a result, we could not include linyphiids in the sample.

The theridiids used in this study build gumfoot lines naturally, so no experimental manipulation was necessary (Fig. 1c). The predatory behavior of the theridiids included in this analysis is well documented. We took the data from videotapes of predatory sequences of 20 adult females of each of the following species: *Achaearanea cinnabarina* Levi 1963 (Japyassú & Jotta 2005), *Latrodectus geometricus* C.L. Koch 1841 (Corrêa & Japyassú 2001), *Achaearanea digitus* Buckup & Marques 2006 (Japyassú & Caires 2008), *Achaearanea tepidariorum* (C.L. Koch 1841) (Macagnan & Japyassú,

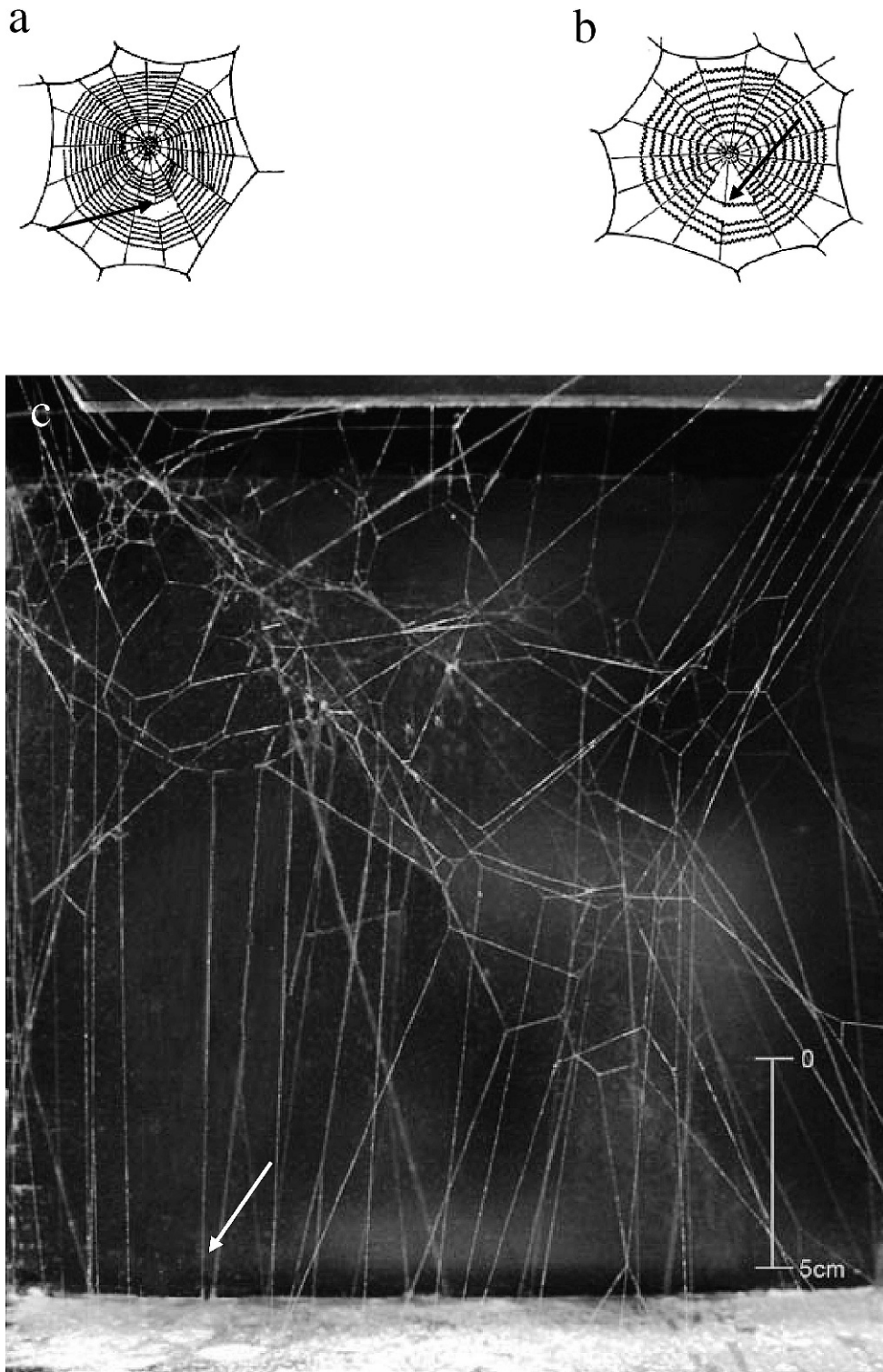


Figure 1.—Pseudogumfoot and gumfoot lines. Pseudogumfoot lines were produced through two different procedures. For ecribellate spiders [Araneidae (*Micratena nigrichelis*, *Alpaida veniliae*, *Metazygia rogenhoferi*, and *Metazygia gregalis*) and Tetragnathidae (two unidentified *Leucauge* species)] a radius was cut in its midpoint (a). For cribellate spiders [Uloboridae (*Zosis geniculata*)] adhesive spirals connected to the freed radius were also cut (b). Webs of theridiids (in the photo, web of *T. evexum*, other species used include *Latrodectus geometricus*, *Achaearanea cinnabarina*, *Achaearanea digitus*, and *Achaearanea tepidariorum*) do present gumfoot lines in natural conditions. The gumfoot lines are the vertical lines connecting the upper sheet to the substrate (c). Arrows point to the place where prey was introduced in the manipulated webs.

Table 1.—Percent of spider responses and mean reeling extent (RE) in the species studied.

Family	Species	RE	Spider responses		
			Full reeling	No reeling	Mixed
Uloboridae	<i>Z. geniculata</i>	59.9	2	9	9
Araneidae	<i>M. nigrichelis</i>	48.5	2	9	9
	<i>A. veniliae</i>	31.5	0	12	8
	<i>M. rogenhoferi</i>	51.9	0	14	6
	<i>M. gregalis</i>	29.0	0	18	2
Tetragnathidae	<i>Leucauge</i> sp 1	61.6	5	7	8
	<i>Leucauge</i> sp 2	41.2	0	13	7
Theridiidae	<i>L. geometricus</i>	82.9	6	8	6
	<i>T. evexum</i>	28.1	0	18	2
	<i>A. cinnabarina</i>	52.8	2	10	8
	<i>A. tepidariorum</i>	100.0	2	18	0
	<i>A. digitus</i>	87.6	13	2	5

unpublished data) and *Theridion evexum* Keyserling 1884 (Garcia & Japyassú 2005).

Phylogenetic analysis.—We used the phylogeny of Griswold et al. (1998) modified at the araneid (Scharff & Coddington 1997) and theridiid (Agnarsson 2004) nodes to reflect the internal relationships within these families. The occurrence, frequency, and degree of predatory reeling in each species was plotted and optimized over the species phylogeny using the software package Mesquite (version 2.0). The ancestral states for the continuous characters were reconstructed with the parsimony method. Since the linear parsimony model does not apply to phylogenies with polytomies, we used the squared parsimony model instead (Maddison & Maddison 2006).

RESULTS

Reeling during the predatory sequence occurred in all species included in the analysis. In all species the spiders touched the gumfoot (theridiids) or the pseudogumfoot (orbweavers) and pulled it with alternate movements of their front legs. In a typical cycle of leg movements, the right leg I was pulled to the cephalothorax, holding the capture line until the next leg (left, II) grasped it, when leg I (right) was put forward, while leg II (left) was pulled to the cephalothorax; this sequence passed orderly through the front legs (I right, II left, I left, II right) only to repeat itself as a cycle until the spider touched the prey hanging on the capture thread. *Zosis geniculata* (Uloboridae) sometimes performed this sequence slowly, so that we could observe that legs III rolled up the capture line (i.e., the experimentally broken radius) as the front legs pulled it, producing a silk pellet as a result. This cycle occurred in all species observed, so this coordination of leg movements, used precisely in the context of prey capture, optimizes at the base of the phylogeny of the whole Orbiculariae group.

We also observed orbwebs that had naturally occurring pseudogumfoot lines, that is, radii that were naturally broken, probably due to the activity of insects, or due to previous prey captures, which resulted in small holes in the orbweb. One of us (CRMG) observed *M. rogenhoferi* (Araneidae) capturing prey ensnared in these naturally broken radii with reeling movements. Although we have also found naturally occurring holes in webs of *Z. geniculata*, these spiders never reeled the prey we offered at the end of the naturally broken radius. It

seems that the cribellate adhesive threads form a strong and resistant net with the broken radius, inhibiting the spider from pulling the broken radius with reeling movements. Thus, in our sample, reeling occurs naturally among cribellate, but not among cribellate orbweavers.

Although all species showed reeling, there was considerable variation among them. The mean extent of reeling (RE) varied in such a way that we could not detect any tendency of increase or decrease of it along the phylogeny (Table 1).

We plotted the degree of mixed responses (the number of individuals with mixed responses, i.e., of spiders that both walked to the prey and reeled the gumfoot in one single predatory bout) on the phylogeny of the clade Orbiculariae. The results clearly indicate that the degree of mixed responses decreases from the root to the tip of the phylogeny. All but one of the state transitions, from ancestral to derived clades, is from a higher to a lower number of mixed responses (Fig. 2). The evolutionary reduction in mixedness occurs independently in two clades: once inside the family Araneidae and again inside the clade subtending Tetragnathidae and Theridiidae. Among araneids the frequency of mixed responses decreases only in favor of the tactic “no reeling,” while in the theridiid lineage, it decreases sometimes in favor of “no reeling” (as in *T. evexum*) and sometimes in favor of “full reeling” (as in *A. digitus*, Table 1).

DISCUSSION

Reeling web threads to capture prey is homologous for all orbweavers. It occurs even in the outgroup of Araneoidea (*Z. geniculata*) when an adequate context (an artificially manipulated web, with a pseudogumfoot - i.e., a loose radius) is present. *Zosis geniculata* (Uloboridae) performs, in all detail, the long coordination of alternate movements of the front legs, exhibiting even full reeling; e.g., it performs a sequence in which the spider starts reeling movements at the hub (where she rests), and stops only when she touches the prey, still at the hub. The predatory reeling of orbweavers (described for the first time in the present paper) is homologous to the previously described theridiid reeling (see, for example, Garcia & Japyassú 2005), because it is used at the same moment in the capture sequence (after detection and before biting the prey), with the same topology of leg movements and with the same function, fulfilling the traditional criteria for primary

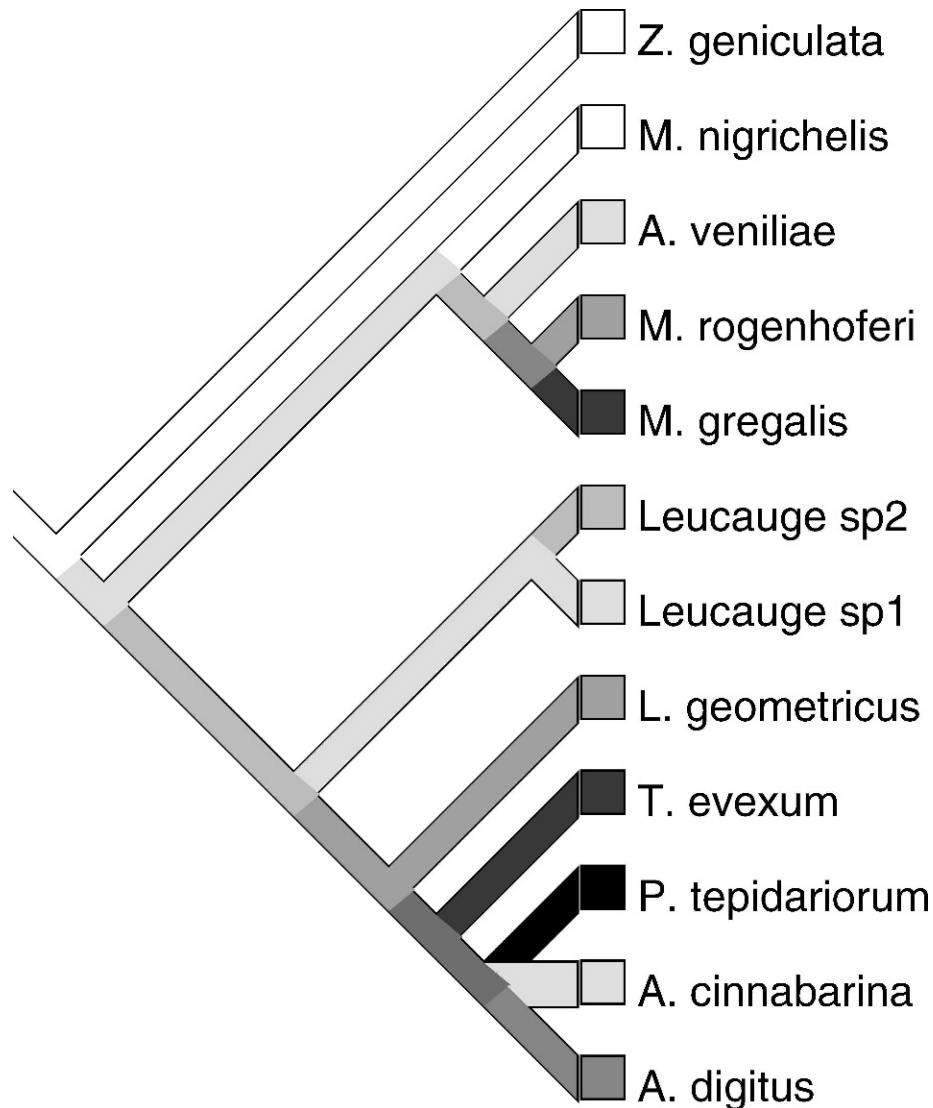


Figure 2.—Evolution of predatory reeling in the clade Orbiculariae. Whiter colors means higher number of mixed responses in the taxon (higher number of individuals performing mixed responses). The number of individuals with mixed responses (i.e., of spiders that both walk to the prey and reel the capture line in a single predatory bout) decreases from ancestral to derived clades.

homology (Wenzel 1992). Also, predatory reeling is congruent with the majority of the other characters used to estimate the phylogeny of the group, since it perfectly fits the phylogeny of Orbiculariae, thus standing also as a secondary homology statement (sensu de Pinna 1991). This should be considered as a provisional (secondary) homology statement since we presently have data for only a few species of orbweavers. Nevertheless, we are confident that reeling will still be homologous when additional species are examined. We have observed other species (not included in the analysis because of the small number of individuals or lack of complete identification), such as the araneids *Acacesia* sp. (2 young specimens), *Araneus* sp. (4 adults), *Eustala* sp. (2 adults, 4 young), *Mangora* sp. (4 adults, 2 young), *Parawixia* sp. (4 young) *Verrucosa* sp. (1 adult), *Gasteracantha cancriformis* (10 adults), *Wagneriana* sp. (1 adult), and also *Tetragnatha* sp. (Tetragnathidae, 6 adults, 4 young); in all of them reeling was present. Reeling occurred even among young spiders in all

species whereupon it was tested (including exemplars of *A. veniliae* and *Leucauge* sp., included in our analysis); an indication that previous experience could be unnecessary for the display of this behavior. Thus, it seems to us that the presence of predatory reeling is strongly supported as a basal feature of Orbiculariae.

Although predatory reeling is a basal feature of Orbiculariae, uloborids (one of the basal groups of Orbiculariae) do not perform it unless we offer them modified webs with pseudogumfoot lines. This is probably a consequence of the cribellate adhesive spiral, a thread that is tough enough to keep the radii firmly in place even when a radius is broken. Thus, the occurrence of predatory reeling in nature is precluded by the very nature of the cribellate adhesive thread. Since predatory reeling does not occur naturally in uloborids, it cannot have been selected for during the evolution of these spiders simply because any trait needs to be at least expressed in order to be selected. Nevertheless, among ecribellate

orbweavers it is expressed, albeit occasionally, in natural conditions: some radii are unpredictably broken by struggling prey that leave holes in the webs, and these broken radii stand as natural pseudogumfoot lines (since the viscid spirals connect the broken radius loosely to the web). So, it seems that the appearance of the viscid, more extensible cribellate adhesive thread (Kölher & Vollrath 1995) has exposed to selection an old but until now unexpressed coordination of leg movements: predatory reeling. Finally, among theridiids, predatory reeling seems to have evolved into a specialized capture tactic, associated with a specialized web structure, the gumfoot.

Although predatory reeling was “present” long before being expressed, it seems that the actual expression of it had an impact on its evolution since the level of mixed responses reduces progressively after its first expression at the base of Araneioidea (Fig. 2). More direct responses, that is, full reeling or full locomotion (of the spider) to prey (instead of a mix of both responses), could be selected for, being quicker or more efficient in subduing the prey, but at the moment we have no data to help tease apart these possibilities. What seems clear is that, in order to have a more direct response, the spider needs to know earlier which tactic to employ in the capture sequence: to move the prey towards herself (full reeling), or to move herself towards the prey. The spider needs to evaluate the situation before making the first move. Thus, more direct responses imply the evolution of some kind of decision-making mechanism in order for the spider to get the information necessary to opt between the two competing tactics as early as possible.

The strong variability in the extent of reeling (RE) among species (Table 1) could be due to differences in starvation. Spiders well fed are more selective as to prey type (Li 2000), so it is possible that feeding condition affects other foraging responses. Nevertheless, this does not seem to be the case because previous results demonstrate that differences in starvation do not affect parameters of predatory reeling (Gonçalves et al. 2006). This variability is probably tied to some ecological condition we did not evaluate.

Origins of reeling outside the predatory context.—Although predatory reeling is a novelty for orbweavers, these spiders do perform reeling movements outside of a predatory context. While building the radii of their orbwebs, spiders from the family Uloboridae (Wiehle 1927; Eberhard 1972, 1990), Araneidae (Peters 1933; Tilquin 1942, p. 195; Eberhard 1982, 1990), Tetragnathidae, Theridiosomatidae, and Anapidae (Eberhard 1982) cut and reel a temporary radius upon laying a permanent one. Theridiids like *Achaearanea tepidariorum* and *Latrodectus geometricus* (Eberhard pers. comm.) also maintain this behavior while building the gumfoot lines of their cobwebs. In another example of reeling, orbweavers that are hanging on a dragline, climb back up it with reeling movements of the front legs, while legs III make a pellet from the dragline (Tilquin 1942, pp. 116–125). Orbweavers also cut and reel threads upon building a silken bridge between two points in order to make the web below it (Tilquin 1942, pp. 140–142). This bridging behavior is also common among non-orbweavers (Deeleman 2007), which make bridges in order to walk from one place to another in the vegetation.

Thus, there are several kinds of reeling among orbweavers, and it is possible that all of them compose a single character with multiple states. If this is the case, predatory reeling could be still another state of this compound character, but at the moment we have no data to support this hypothesis.

Implications for the evolution of context dependent behaviors.—Our results point to an evolutionary path that starts with a behavior that cannot be a predatory adaptation (since it is not expressed in predatory events), one that is later exposed to selection via evolutionary changes in the context (cribellate orbweb) of its expression, and finally, through further changes in this context (gumfoots of cobwebs), become an adaptation. The evolution of this new prey capture tactic (reeling) did not result from the evolution of any new coordination of motor actions. The coordination of the movements needed to reel the prey was already in place when it was first expressed with a predatory function. Instead, reeling required the evolution of an adequate environment, or context, for its appearance (a pseudogumfoot, i.e., a loose radius). To our knowledge, this is the first report of an evolutionary change due to a change in the context of expression of the trait, not to a change in the trait itself.

There is abundant literature on the evolution of one behavioral trait as a response to the previous evolution of other behavioral traits; more precisely, as a response to the extraorganismal effects of these previous behavioral traits. Odling-Smee et al. (2003) extensively review this literature, naming these behaviors (with extraorganismal effects) niche-construction, and they argue for a kind of pleiotropic connection between the two behavioral traits, a connection that is mediated by the external effects (the “extended phenotype”) of the ancestral behavioral trait. This niche-construction perspective certainly grants evolutionary power to the context of occurrence of a behavior with non trivial outcomes such as the maintenance of polymorphic equilibria, or even the fixation of otherwise unfavored alleles [see Odling-Smee et al. (2003) for the results of different evolutionary simulations under different modeling assumptions, pp. 133–166], but in the present paper we are not dealing with niche construction but with a different phenomenon.

In all niche-construction models a niche-constructing behavior (such as nest construction among *Gasterosteus* or cichlids) alters the environment, and this new environment acts as a selection pressure for the appearance of other, derived behaviors (such as elaborate courtship rituals in the examples above - McLennan et al. 1988, Odling-Smee et al. p. 95). In the case of predatory reeling, we are dealing with an instantaneous event: *Z. geniculata* never uses predatory reeling in nature, but if you provide an artificially modified web (with a loose radius) she immediately uses this new behavior. So, there is no time for selection to mold this new predatory tactic (reeling), which is simply a result of a plastic behavioral system exposed to unexpected conditions. It is only after reeling appears regularly in the repertoire of orbweavers (after the loss of the cribellum among Araneioidea), that selective forces can help to mold this new tactic.

This should not be considered an unusual, but rather an unexplored evolutionary scenario. Studies show that spiders can behave in atypical ways when subjected to atypical conditions. Gundermann et al. (1993) observed unusual social

behavior in a typically solitary species when the spiders were forced to live under unusually high densities. Roland et al. (1996) show that maternal behavior can be induced experimentally outside its normal conditions of occurrence. These phenomena fall into the general category of behavioral plasticity, but in these cases we are dealing with the study of plasticity outside the normal range of the species' ecological conditions, outside the normal population density, outside normal conditions for maternal care, or outside the normal web conditions (present study). Thus, the evolution of reeling suggests a new mechanism for the production of evolutionary novelties, that is, the exploration of unusual ecological conditions and of the regular effects that these abnormal conditions have on phenotype expression.

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