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Fishing for Prey: the Evolution of a New Predatory Tactic Among Spiders (Araneae, Pholcidae)

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Pholcus phalangioides is a versatile predator. Besides capturing prey entangled on its sheet web, it invades heterospecific webs, where it preys upon insects, eggs and the resident spider. This spider shows still another predatory tactic: we have observed it catching cursorial prey outside its sheet web. This is possible because of the existence of gumfoot lines in the sheet webs of some pholcid spiders, a feature previously observed only among theridiids (a distant, unrelated spider family). This web feature was observed in *Pholcus phalangioides*, *Smeringopus pallidus* and *Physocyclus globosus*, but not in *Mesabolivar cyaneotaeniatus* or in another unidentified *Mesabolivar* species. Based on these observations we suggest that gumfoots are basal in pholcid phylogeny. Some predatory behaviours typical of theridiid spiders also occur among these gumfoot building pholcids (reel and ground-search); sticky-silk wrap attack occurs in all pholcids observed so far. We describe the predatory sequence of *P. phalangioides* when using gumfoot lines, and discuss possible behavioural homologies between pholcids and araneoids. We also discuss the evolutionary implications of these findings.

Index terms: Foraging behaviour. Web pattern. Web building. Behavioral evolution. *Pholcidae*. Spiders.

Pescando a presa: a evolução de uma nova tática predatória em aranhas (Araneae, Pholcidae). Além de capturar presas em sua teia, a aranha *Pholcus phalangioides*, um predador versátil, invade teias de heterospecíficos, onde se alimenta de insetos, de ovos ou de aranhas residentes. Esta aranha apresenta ainda outra tática predatória: observamos a captura de presas cursoriais fora de sua teia em lençol. Esta tática é possível devido à presença de fios âncora que partem do lençol e que apresentam sapatas adesivas na região de contato com o substrato. Tal estrutura, relatada previamente apenas para as distantes e não aparentadas aranhas da família Theridiidae, é registrada pela primeira vez em aranhas da família Pholcidae: *Pholcus phalangioides*, *Smeringopus pallidus* e *Physocyclus globosus*, mas não em *Mesabolivar cyaneotaeniatus* ou em outra espécie não identificada de *Mesabolivar*. Baseado na distribuição destas estruturas entre as espécies da família e em correlações entre o comportamento e a morfologia das fiandeiras, sugerimos que estas estruturas são evolutivamente basais na família Pholcidae. Alguns comportamentos predatórios típicos de theridiídeos, como pesca e busca, também ocorrem nos pholcídeos que constróem sapatas adesivas; o ataque por enrolamento com seda viscosa ocorre em todas as espécies de pholcídeos observadas até o momento. Descrevemos a seqüência predatória de *P. phalangioides*, e discutimos possíveis homologias entre pholcídeos e theridiídeos assim como as implicações evolucionárias destas descobertas.

Descritores: Forrageamento. Estrutura da teia. Construção da teia. Evolução comportamental. *Pholcidae*. Aranhas.

Behaviour has been progressively used in phylogenetic studies (De Queiroz & Wimberger, 1993; McLennan, Brooks, & McPhail, 1988; Prum, 1990; Scharff & Coddington, 1997; Slikas, 1998). But behaviour, unlike morphology, do not have a long lasting tradition of debates among researchers concerning the definitions and the delimitation of the observed structures, so that researchers not always agree on what precisely are the limits of the behavioural categories they employ. This is indeed a problem about a basic question in

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evolutionary analyses, that is, the statement of homology.

Therefore, it seems necessary a comparative approach and a revision of the available descriptions in order to discuss these categories on common grounds. This is also important in order to hypothesize primary homologies (*sensu* de Pinna, 1991, 1997), that is, topographical similarities based on Remane's criteria of homology (adapted to the behavioural domain – see Greene, 1994). This is specially important if the behavioral unit is variable within a species, that is, if there is plasticity in behavioral expression.

Pholcid spiders are known as versatile predators. *Pholcus phalangioides*, for example, not only captures prey entangled in its web, but also invades heterospecific webs, where it eats insects and eggs, and uses aggressive mimicry tactics to prey upon the resident spider (Jackson & Brassington, 1987). It captures efficiently a wide variety of prey (Nentwig, 1983) and shows great behavioural plasticity when preying upon these taxa (Groppali & Senna, 2000; Jackson & Brassington, 1987). Also, pholcids such as *Pholcus phalangioides* (Zunino, Groppali, Laudani, & Priano, 1996), *Modisimus* sp (Eberhard, 1992b), *Holocnemus pluchei* (Sedey & Jakob, 1998) and *Physocyclus globosus* (Eberhard, 1992a) are known to weave regular or irregular sheet webs. Some species add small, delicate sticky-balls to the sheet-web (Briceño, 1985; Zunino et al., 1996).

Laboratory observations revealed that some pholcids could have yet another predatory tactic in its repertoire. *Pholcus phalangioides* captured prey walking below or nearby, but clearly outside the sheet. To understand how this could happen, we investigated the structure of the capture web of some pholcid spiders, and also detailed the predatory behaviour of *P. phalangioides* outside its sheet.

We compare the present findings with the predatory behaviour of other spiders and discuss the homology status of predatory sequence elements. We also discuss the evolutionary implications of the present findings.

Methods

Collection and Maintenance

Voucher specimens of the observed species are deposited at Butantan Institute. *Pholcus phalangioides* were collected at Butantan Institute (São Paulo – SP: IBSP27654, IBSP27653, IBSP27652, IBSP27642, IBSP27649, IBSP27641, IBSP27648); *Smeringopus pallidus* at São Paulo University (São Paulo – SP: IBSP27657, IBSP27647, IBSP27645, IBSP27656); *Mesabolivar cyaneotaeniatus* at Mairiporã (SP: IBSP27650, IBSP27646, IBSP27640), and *Physocyclus globosus* at Piracicaba (SP: IBSP33010, IBSP33011, IBSP33012, IBSP33013). The spiders were housed in acrylic laboratory cages (20x20x20cm), where the web structure was observed and photographed. The specimens were offered weekly a nymph of *Gryllus sp* (Orthoptera). Gumfoot and sheet threads were collected and observed in an optical microscope.

Predatory behaviour

The predatory sequence of twenty adult *P. phalangioides* (13 females and 7 males) was videotaped with a miniDV camera (Canon XL1), one sequence for each specimen. At the beginning of the sequence, prey was left onto a gumfoot; if it escaped from the gum droplets, we allowed it to move around at the floor of the cage, until it got ensnared in other gumfoots. Each session ended after the spider paused, ingesting the prey for five minutes (at any place in the web). Alternatively, the session was ended after the spider remained with the captured prey for five minutes in the initial resting-place.

Spiders were offered *Gryllus sp* nymphs; spider/prey relative body size varied from two to one. As web density increases and gumfoot adhesiveness diminishes with time (person. obs.), data was gathered only from two to four week old webs. To control for spider hungriness, all spiders were starved for one week before the experiment. We thus controlled for prey type and size, web quality and spider hungriness, and this was done in order to reduce predatory sequence variability, and to improve the statistical description of behaviour (Japyassú & Viera, 2002).

Analysis of behavioural sequences

The predatory sequence was divided in four successive phases: (1) *detection*, from the beginning of the sequence until the first touch at the prey; (2) *hanging-immobilization*, from the preceding phase until the fixation of the wrapped prey on the upper sheet; (3) *sheet-transport*, comprising the transport of prey, within the sheet, to the initial resting place (where the spider rested at the beginning of the sequence) and (4) *ingestion*, from the preceding phase to the end of the session. During this last phase the spider starts feeding on the prey.

The sequences were transcribed with the software Observer Video-Pro (Noldus, Trienes, Hendriksen, Jasen, & Jansen, 2000) and transformed into four preceding-following categories transition matrix, one to each predatory phase.

Preliminary analysis of these matrices showed no significant difference between male (N = 6) and female (N = 14) predatory behaviour (U = 27,000; P = 0.239). Due to this preliminary analysis, we decided to pool together data from both sexes.

Only significant behavioural transitions were used in the quantitative description of the predatory repertoire (P < 0.02, Bishop, Fienberg, & Holland, 1975). We pooled the 20 individual matrices and emptied the main diagonal (self-repeating categories were disregarded). These analyses were performed separately for each of the four phases of the predatory sequence, with the aid of the program Matman (De Vries, Netto, & Hanegraaf, 1993).

Results

We show for the first time the existence of gumfoot capture lines, a characteristic feature of spiders from a distantly related family (Theridiidae), in the web of pholcid spiders (Pholcidae). We have also recorded the building

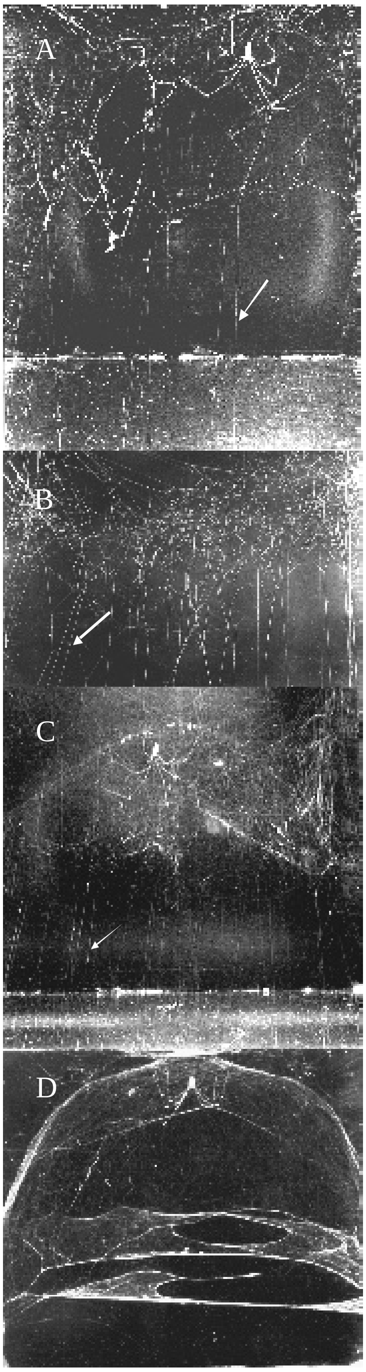

Figure 1. Overview of the web of pholcid spiders. Arrows point to the gumfoot lines. (A) *P. phalangioides*, with various gumfoots at the bottom of the picture. (B) *P. globosus* (gumfoot lines visible, but not its adhesive band). (C) *S. pallidus*, with gumfoot lines barely visible, and (D) *M. cyaneotaeniatus* without gumfoot lines. Bars equal to 1cm.

of these gumfoot lines and its use during predatory bouts in *Pholcus phalangioides*. Thus some pholcid traps have at least two distinct capture surfaces: the sheet and the gumfoot field, which comprises the areas to which gumfoots are attached.

Web structure

The web of *P. phalangioides* consists of a loose upper sheet surrounded by vertical gumfoot lines, which are fixed at the lower substrate (fig.1a). The form of this sheet varies with the supporting structures. It is generally horizontal and in our lab cages usually concave, with the concavity facing downwards. The sheet converges to a retreat at an upper corner, wherein the spider usually rests; this retreat is like a silken tube with wide-open meshes, especially at its lower part, where the openness of this mesh is extreme. The gumfoot lines usually depart from the periphery of the sheet, sometimes from the lower part of the retreat; we have observed gumfoots not only in lab webs, but also in outdoors and indoor webs. There are plenty of threads connecting the sheet to upper supports, sometimes as many of these threads as to obscure the sheet pattern, making it look like as if there was no sheet, but a three dimensional net instead. There are also a few supporting threads similar to gumfoot lines (but with no viscid droplets onto it), connecting the sheet straight to the lower substrate. Each gumfoot line has a long adhesive band (*c.* 0.5cm; fig.2a) at its distal extremity (*i.e.* at the far end from the sheet). The adhesive band is constituted of several consecutive small droplets, which may also occur at some of the lines that constitute the sheet. Although gumfoot lines are generally fixed at the lower substrate, they can sometimes be fixed at lateral substrates, always below the sheet.

The web of *P. globosus* seems in all respects a reduced *P. phalangioides* web, with an upper, sometimes concave sheet, which varies in form according to the surrounding supporting structures, and with gumfoot lines scattered around the periphery of this sheet (fig.1b). It also presents other *P. phalangioides* web features: a clearly delimited retreat fixed at an upper

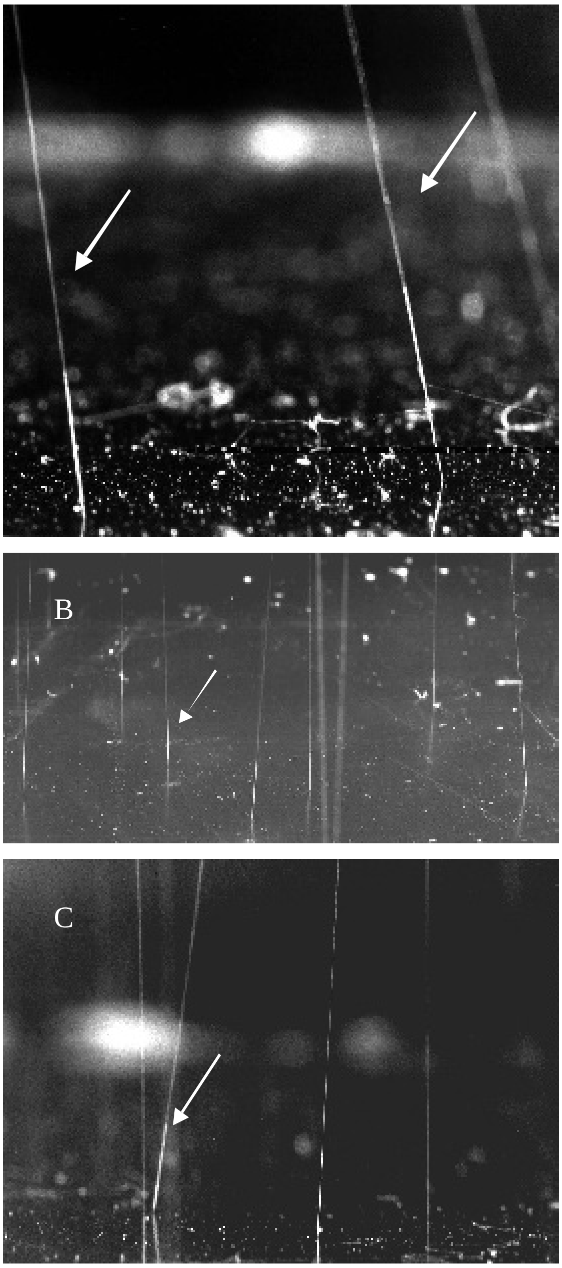

Figure 2 Overview of the adhesive band of gumfoot lines of pholcid webs. (A) *P. phalangioides*, (B) *P. globosus*, and (C) *S. pallidus*. Arrows point to the beginning of some adhesive bands.

corner; structural, dry threads connecting the sheet strongly to upper supports and, less frequently, to lower ones; and viscid droplets scattered throughout the sheet. The gumfoot lines present a delicate, small basal adhesive band (fig. 2b).

The web of *S. pallidus* presents a more regular sheet, usually concave and with a wider mesh than that of *P. phalangioides* (fig. 1c). The spider rests near the apex of the concavity and, although she usually returns to this same sheet area after capture sequences, there is no conspicuous retreat (the sheet never touches the substrate). The sheet is surrounded by vertical gumfoot lines with basal adhesive bands (figs. 2c, 3). Young *S. pallidus* decorate the web with numerous small white fluffy silken balls scattered on the upper portion of the sheet; these white balls decrease in number as the spider grows, and some adults even stop its production.

The webs of *M. cyaneotaeniatus* do not present the sticky gumfoot lines. Its sheet is concave, with no retreat, and the spider rests at its apex (as in *S. pallidus*; fig. 1d). The sheet mesh is fine grained, with viscid droplets scattered on it. It is frequently found in tropical rain forests at 0.5-1.5m from the litter, between leaves and tree branches. Contrarily to the previous species, *M. cyaneotaeniatus* was never observed around human dwellings.

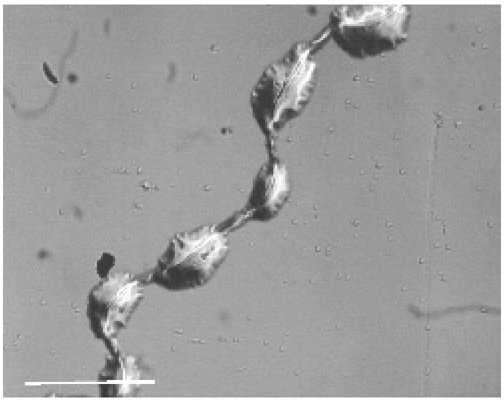

Figure 3. Optical microscope detail of the adhesive band of the gumfoot lines of *S. pallidus*. Bar equal to 0.1mm.

Gumfoot building

P. phalangioides was observed building gumfoot lines during predatory sequences. This usually happened after a long, unsuccessful detection phase: sometimes the prey frees itself from gumfoot droplets, and the spider either halts at the periphery of the sheet or searches fruitlessly for the prey in the cages' floor (ground-search). All this can be repeated over and over as the prey escapes from successive gumfoots, and eventually the spider begins to build new gumfoot lines. These new gumfoots are more effective at detaining the prey than the older, less adhesive ones.

Although gumfoot building was observed mainly at the detection phase, possibly as a way to better entrap the prey, it also occurs after prey immobilization. If the capture and immobilization process spans for a long time, the spider will make repairs in the web and build gumfoot lines at the sheet transport phase, sometimes even while seizing the prey with the chelicerae.

In order to build a gumfoot, the spider fixes at the border of the sheet and descends to the substrate grasping nearby gumfoot lines (leaving a silken line behind, fig.4a). When she touches the substrate (with legs I, II and III), still grasping a gumfoot line with one of the fourth legs, she fixes the new gumfoot (stretching the line with the other fourth leg before fixing, fig.4b). She then returns upwards (still paying out a line, figs.4c and 4d), fixing once to the just laid gumfoot line nearby the sheet border. Thus, the gumfoot consists of two joined silk threads. The spider's abdomen moves in a distinctive slow fashion while laying the basal glue droplets, which are laid only after the attachment to the substrate, while the spider is moving upwards toward the sheet.

We call "fishing" the consecutive use of routines such as "building gumfoots", tug and reel, because of the obvious similarity of this procedure with human fishing.

Categories of behaviour

Some behavioural categories were already described in spider behaviour literature, such as bite and short-bite, fix, cut silk, touch,

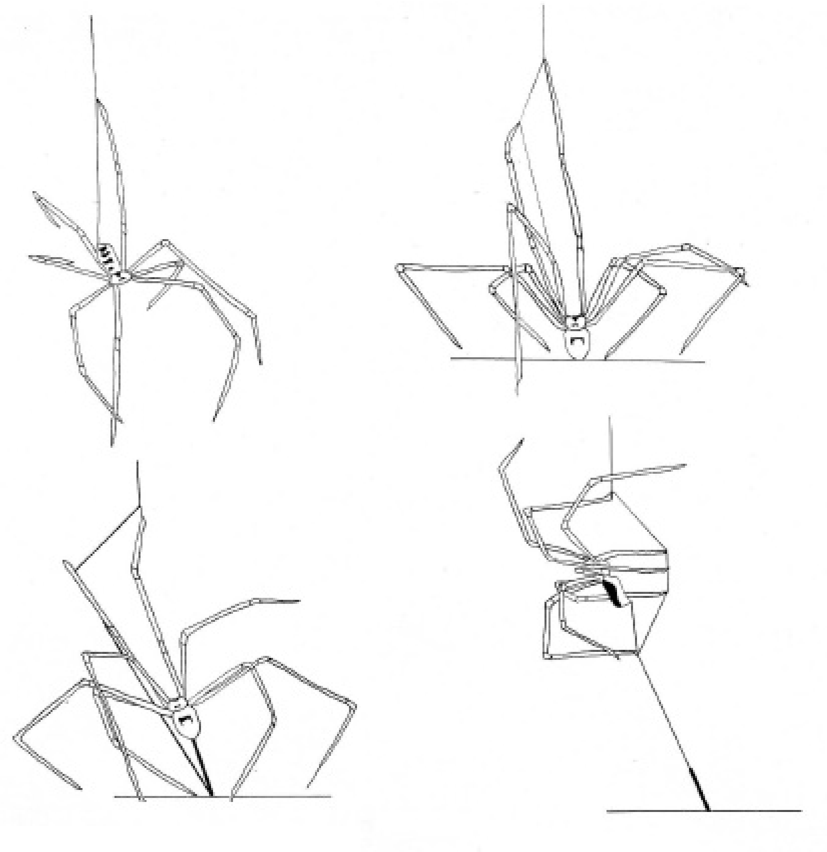

Figure 4. *P. phalangioides* building a gumfoot.

retrieve, manipulate, approach, wrap, pause (Robinson & Olazarri, 1971; Viera, 1983, 1986, 1994), wrap attack (Eberhard, 1982; Robinson, 1969), sticky-silk wrap (SS-wrap; Coddington, 1986), tug, abdomen-twitching, bouncy-walking (Jackson & Blest, 1982; Jackson & Brassington, 1987), carry-on-silk, (Groppali & Senna, 2000), fix and rotate, grooming (Japyassú & Viera, 2002), reel, pay-out-line (Garcia & Japyassú, *in press;* Japyassú & Caires, *submit.*). These categories are described in the appendix. Some authors describe *P. phalangioides*' use of behavioural categories not observed in the present study, such as tense, shiver (Jackson & Brassington, 1987) and whirl (Jackson, 1992; Jackson et al., 1990; Jackson, Rowe, & Campbell, 1992;), and these behavioural categories seem not to be used during foraging.

Behavioural categories included in the predatory repertoire and reported for the first time in this paper are defined below, and include, ground-search, grope, pull-out-prey and return.

Ground-search (gr-search): in order to locate the prey (which has escaped from the gumfoot, but is still nearby), the spider, hanging upside-down on the gumfoot lines, repeatedly touches the lower substrate with front legs (I and/or II). As soon as she finds the prey, the spider rotates its body in order to wrap it (SS-wrap); if she still can't find the prey, she may search for it again, now with legs III and IV. The leg touching the prey may sometimes bring it near the spinnerets before SS-wrap.

Grope: this category is more frequent among theridiids (for example, *Achaearanea tepidariorum*, *A. cinnabarina*, *Latrodectus geometricus*, *person. obs.*), but also occurs among pholcids. After storing the immobilized prey, the spider can perform various activities, such as build new gumfoot lines, groom or walk with its characteristic bouncy manner, so that she needs to locate the prey afterwards. To do so, the spider simply moves laterally one of its legs until she touches the line the prey is hanging on; after locating the prey she usually touches and retrieves it. Jackson et al. (1992) describe, for *Smeringopus pallidus* and *Psilochorus sphaeroides* (pholcids), a sequence quite similar to the above description of grope. However, they include it within their category whirl. We prefer to dissociate *grope* from whirl since both behaviours can occur independently. Grope seems to serve always the same function both in the predatory context of the present paper and in the aggressive mimicry context of Jackson et al. (1992): it possibly works as a mean to find either the prey or the predator.

Pull-out-prey (pull): while the spider is wrapping the prey at the bottom of the gumfoot line, she tries, and sometimes succeeds, to pull out the prey from the capture site, so as to carry it on silk, to the upper sheet. In this pull-out-prey routine the spider, usually in wrapping posture (legs I grasp the upward portion of the gumfoot, and legs II hold the same or nearby gumfeet, legs III hold the prey while legs IV throw silk onto it), flexes simultaneously legs I (sometimes also legs II) and III (wrapping may continue or halt). In a variant of this behavioural category, the spider is in this same wrapping posture and stops wrapping movements to place legs IV onto the floor; she then flexes legs I and III and extends legs IV so that the spider's and prey's bodies move upwards. In still another variant, the spider, completely onto the floor, extends legs I, II and IV (placed on the floor) and flexes legs III (holding the prey), so that, again, spider's and prey's bodies move upwards.

Return: the spider may be unsuccessful in a capture attempt (prey not successfully immobilized, frequently not even located), and in this case she returns to the sheet or resting place, usually with bouncy movements.

Predatory sequence

Some pholcids use a unique prey capture technique in the family: the sticky silk wrap attack (ss-wrap). Prey reeling (another behaviour previously unreported in the family) usually precedes this technique. These behaviours occur in all the gumfoot building pholcids herein studied and also in an unidentified *Metagonia* species. *M. cyaneotaeniatus* and another unidentified *Mesobolivar* species also use the ss-wrap in captures of preys at the sheet portion of the web (*person. obs.*). We detail below the predatory sequence of *P. phalangioides* (fig. 5).

Detection phase. As soon as the prey gets ensnared at gumfoot droplets the spider tugs several times (intercalating abdomen-twitches between successive tugs). She may not succeed finding the prey (fig.5a, dashed category boxes), and in this case she will return to the resting-place and restart the procedure or, alternatively, after many unsuccessful attempts at locating the prey she will initiate gumfoot building. At successful sequences the spider will approach the prey and *reel* it at a distance. If it is difficult to locate the prey (prey's behaviour varies with predator tactics, but usually *Gryllus* sp nymphs alternated quiescent moments with bouts of runaway attempts), the spider may alternatively ground-search for it at the cage´s floor, touch it and proceeds to the hanging immobilization phase with a ss-wrap.

Hanging immobilization phase. After the ss-wrap the spider wraps the prey with dry threads at the capture site (fig. 5b). In order to carry the prey to the upper sheet she first frees it from the web either pulling it out with legs or cutting the gumfoot line above and below the prey. If carry-on-silk includes bouncy walking movements (bw-transp), the prey is fixed to the sheet right after the spider reaches the upper sheet; if not, the spider does bouncy walking movements at the sheet before fixing the prey to the sheet. If the detection phase is long, the spiders include bites in the immobilization procedure. If the prey gets entangled while being carried on silk, the spider will perform sequences of pay-out-line/fix/retrieve and then resume transportation.

Sheet transport. After storing the prey and fixing it variously at the sheet, the spider will follow any of two behavioural schemes before applying a bite (grey box, fig. 5c) and proceeding to the ingestion phase. In the first scheme (left portion of the diagram) the spider will perform kind of "resting" activities (at the storing place), such as pause and grooming, before retrieving the prey to apply the bite. In the other scheme (right side of the diagram) the spider simply touches and manipulates the prey before the bite.

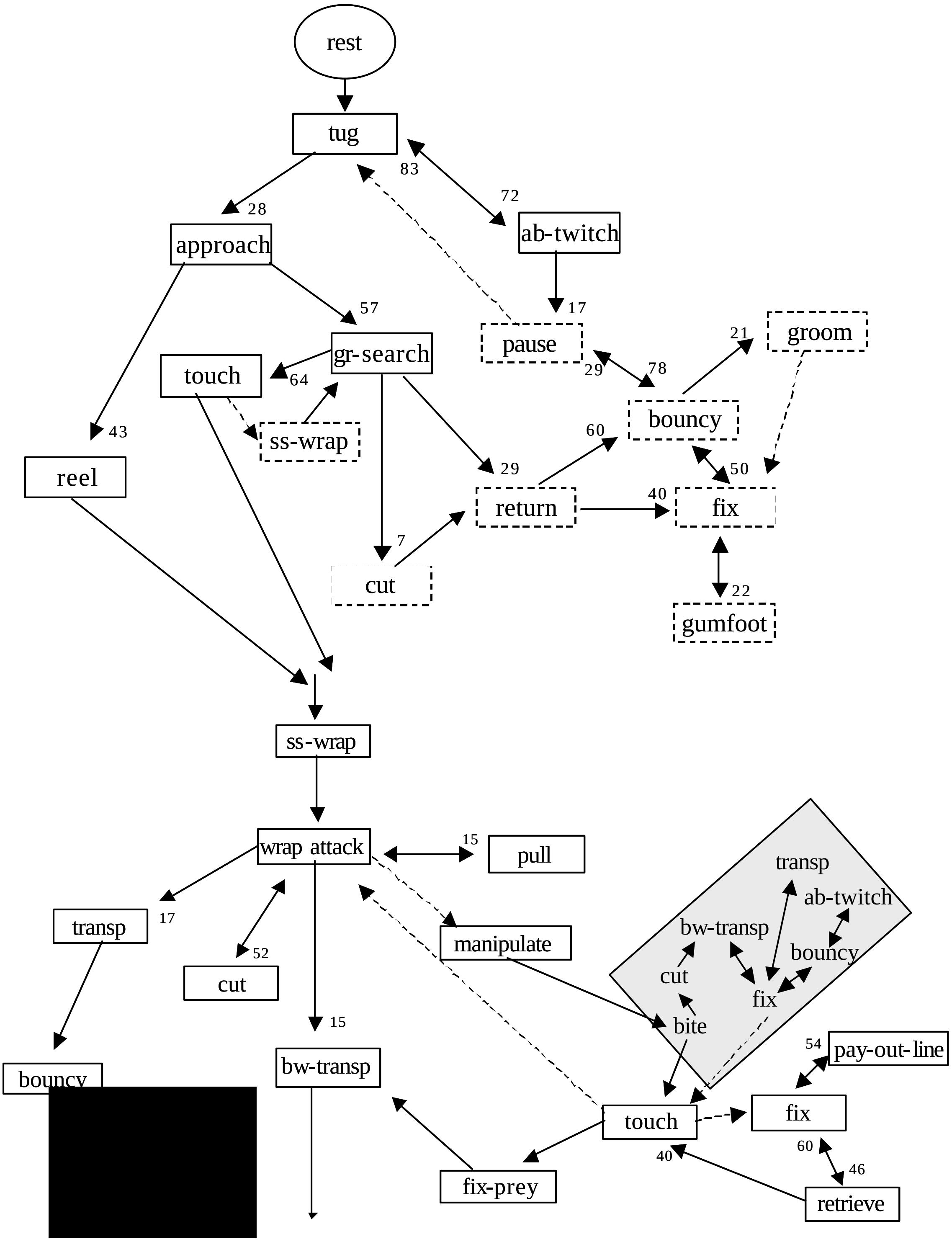

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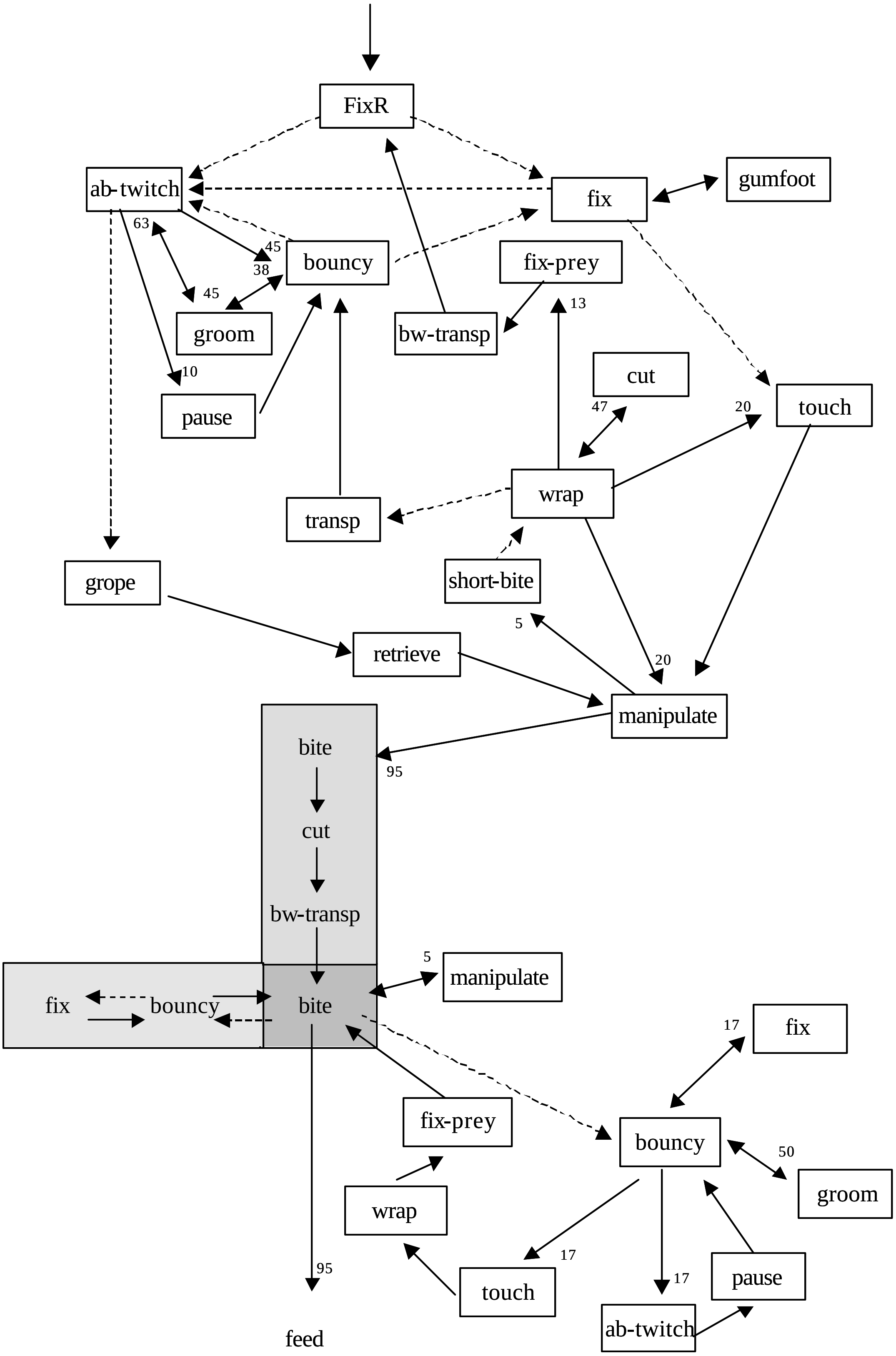
Figure 5. Predatory behaviour upon *Gryllus* sp nymphs walking onto *P. phalangioides* gumfoot field. Dashed arrows represent the most frequent, but non-significant transitions. Numbers near the arrows indicate the percentages of significant transitions; arrows without numbers occurred in 100% of the significant transitions. Grey boxes indicate categories performed along with a sustained bite. (A) Detection phase. (B) Hanging immobilization phase. (C) Sheet transport phase. (D) Ingestion phase. See the appendix and results for the mnemonics and the description of the behavioral categories.


FixR
ab-twitch
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fix-prey
bouncy
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ab-twitch
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In between these two behavioural schemes the spider can wrap and relocate (via carry-on-silk or bw-transp) the prey to another place in the sheet (central portion of the diagram). This wrap-relocate procedure connects the two behavioural schemes just described, and allows much more complex sheet-transport sequences.

In any case, after biting the spider will *cut* the thread connecting the prey to the sheet and take it to the feeding place (with a sustained bite).

Ingestion. At this phase the spider simply sustains the bite while feeding (fig. 5d). Sometimes the spider will manipulate the prey just to bite it again, and in one case (right side of the diagram) she performed those "resting" behaviours (pause, grooming) before wrapping the prey and proceed to the final bite.

Discussion

Previous web structure descriptions

Previous descriptions of web structure and web building in *P. phalangioides* (Kirchner, 1986; Zunino et al., 1996), do not conform to our own observations. We report for the first time the existence of sticky silk gumfoot lines in the web of this spider and, to our knowledge, in the whole family. This structure was up to now restricted to an unrelated spider family (Theridiidae) and is a specialization to the capture of cursorial prey (Foelix, 1996, p. 125).

It seems unlikely that previous authors have worked with distinct species incorrectly identified as *P. phalangioides*. Although pholcids are a diverse group, sometimes difficult to identify even at the generic level (Brignoli, 1981), and with many new species recently described (Huber, 2000), the genus *Pholcus* in particular is well defined, and *P. phalangioides* is a well known spider, quite common inside human dwellings world-wide.

Some spiders flexibly adjust their predatory strategies to available prey (*Parawixia bistriata*, Sandoval, 1994), and *P. phalangioides* is well known for its predatory versatility (Jackson & Brassington, 1987). The presence of potential prey affect not only the timing of web building activities (*Zygiella x-notata*, Pasquet, Ridwan, & Leborgne, 1994), but also its structure: *P. phalangioides* adds more threads to its sheet if prey is offered than if not (Roush & Radabaugh, 1993). Thus, there is a possibility that the building of gumfoot lines in *P. phalangioides* is a conditional predatory tactic, one that is used depending on the local availability of cursorial prey. Nevertheless, this seems for us an unlikely hypothesis to explain the absence of gumfoot lines in European *P. phalangioides*' webs, since Nentwig (1983) shows that cursorial, unwinged Formicidae are the main item in the diet of European populations of this spider. Also, specimens of *P. phalangioides* fed only at the sheet portion of the web continued to build gumfoot lines even when this no-cursorial-prey condition persisted for a 60 days observation period (*person. obs.*).

The last, and most plausible possibility, is that the disjunct European and South-american *P. phalangioides* populations vary as to its foraging adaptations. Geographic variation in spider behaviour has already been documented (Hedrick & Riechert, 1989; Jackson, Li, Fijn, & Barrion, 1998), and this hypothesis remains to be tested in this spider species.

Comparative data and behavioural homologies

Previous accounts of *P. phalangioides*'s predatory sequence (Groppali & Senna, 2000; Jackson & Brassington, 1987) do not describe the use of gumfoots. The gumfoots in *P. phalangioides* are associated to behavioural categories such as reel, ground-search, pull and ss-wrap. These behaviours and others herein described occur among the distantly related orbweavers and theridiids (araneoids), and bellow we provide a comparison with these descriptions (for araneids see Eberhard, 1982; Robinson, 1969; Robinson & Olazarri, 1971; Viera, 1983, 1986, 1994; for tetragnathids see Japyassú & Viera, 2002; for theridiids see Coddington, 1986; for theridiids we also relied upon unpublished data on *Latrodectus geometricus, Achaearanea tesselata, A. tepidariorum* and *A. cinnabarina*).

Web plucking at orbweavers should be scored as a primary homologue to pholcids' (Jackson & Brassington, 1987) and theridiids' tugging. Both behavioural categories seem to have the same function (to locate the prey), they occur at the same point in the capture sequence, and include the same body and leg movements (despite the radically different web structures onto which they occur). Also, detect (Groppali & Senna, 2000) and tug (Jackson & Brassington, 1987) seem to describe the same behaviour in the same spider species, and thus should be taken as synonyms.

Prey reeling occurs in other pholcids, such as *Smeringopus pallidus, Physocyclus globosus,* and an unidentified *Metagonia* species and among theridiids (*person. obs.*). Reeling depends on the existence of gumfoot lines, and thus can occur only among pholcids and theridiids. *Smeringopus pallidus reels* many consecutive gumfoot lines until she locates the prey and brings it to the sheet, hanging on the gumfoot line, whereas the other spiders *reel* less frequently: they usually descend through gumfoot lines to touch the prey and proceed to immobilization. In any case, reeling presents the same sequence of movements and occurs at the same moment in the capture sequence.

Ground-search occurs after the spider moves downward through the gumfoot line; this is frequent among *P. globosus, P. phalangioides* and theridiids. Orbweavers also search for its prey (as soon as it hits the web), but this was described as web plucking (Robinson & Olazarri, 1971), which differs markedly from ground-search. Plucking occurs right after prey contact in the web (spider at resting-place), and ground-search occurs right before prey immobilization, while the spider is outside the trap. Thus ground-search occurs in pholcids and theridiids, and does not exist among orbweaving araneoids which, to our knowledge, have not been observed to look for prey items outside its web.

SS-wrap is a predatory technique previously restricted to a monophyletic spider group [(Theridiidae, Nesticidae) (Synotaxidae, Cyatholipidae)], a clade embedded within the distantly related araneoids (Griswold, Coddington, Hormigas, &Scharff, 1998). We report here its occurrence among pholcids, and not only while the spiders subdue the prey ensnared at gumfoot lines (*P. phalangioides, P. globosus, S. pallidus, Metagonia* sp.), but also while they subdue the prey ensnared at the sheet portion of the web (all pholcids above *plus M. cyaneotaeniatus*). Thus, the use of ss-wrap attack seems to be a primary homology between pholcids and theridiids. The presence of glue droplets is particularly difficult to be observed in the fast wrapping movements and, since it does not depend on the existence of gumfoot lines, it is possible that careful observations reveal the occurrence of this behaviour in other spider families.

Pull-out-prey is not frequent among theridiids, and at this family it is closely associated to carrying the prey on silk (*person. obs.*). After wrapping the prey at the base of the gumfoot, the spider fixes the silken line to it and proceeds upwards, which sometimes results in disconnecting the prey from the gumfoot base (pull-out-prey). Pholcid pull-out sequence is similar to the theridiid one but for the presence of marked leg flexions (see description at the appendix). Among araneids and tetragnathids there is a behaviour (pluck out prey) with this same function (freeing the wrapped prey from the web), occurring at the same moment in the capture sequence (right before carrying the immobilized prey to the feeding place), but with a distinct choreography. Instead of pulling the prey with flexions of the hind legs, these spiders extend their legs while holding the prey with the chelicerae, forcing the wrapped prey out of the web. Thus, pholcid and theridiid pull-out behaviour seems morphologically closer to each other than to araneid and/or tetragnathid pluck out behaviour. The distinct choreographies (pull-out vs. pluck out) are probably the result of the also distinct attack behaviour (ss-wrap vs. bite) of these same spiders, and should be considered as alternative states of a primary homologue behavioural pattern.

Pholcids and theridiids frequently bite their prey only after it has been taken away from the capture site, while orbweavers usually bite them at the capture site, before carrying them on silk. Spiders usually carry their prey in the same manner, the wrapped item hanging from the fourth leg and the spider walking back to the retreat/hub. Nevertheless, the way of carrying a prey item varies with its size (Japyassú & Viera, 2002), and the above considerations refer to a single prey with a size similar to the spider's body.

The behavioral category pay-out-line (see description at the appendix) occurs among theridiids and resembles the orbweavers' line-laying. After wrapping and carrying the prey, the orbweavers usually lay a line before storing it at the hub, that is, they push the prey away with their fourth legs, paying a line behind. Pay-out-line usually occurs after a wrapping bout, but instead of pushing the prey away, it is the spider that moves up through gumfoot lines, leaving behind the prey fixed to a line. Despite their functional and topographical similarity, pay-out-line and line-laying show considerable variability among and within taxa, so that their status as homologues deserves further scrutiny.

Orbweavers and theridiids fix and rotate, in order to store their wrapped prey at the hub, with a behavioural choreography (the spider fixes several times at the hub/retreat while rotating its body sagitally in order to face the prey) not performed by pholcids, which simply fix the hanging prey at the sheet. Also, unlike araneoids, pholcids fix its prey not only at the hub/resting place, but also at other positions in the sheet.

Evolutionary implications

Notwithstanding the scarce comparative information about gumfoot lines and associated predatory behaviours among pholcids (reel, ground-search, pull), its presence in the majority of the taxa investigated so far (*P. phalangioides, P. globosus, S. pallidus, Metagonia* sp.) suggests that this may be a basal condition in the family. This is clearer in the case of *ss-wrap*, another gumfoot related behaviour, and one that occurs even among non-gumfoot building pholcids, such as *Mesabolivar cyaneotaeniatus* and an unidentified *Mesabolivar* species. Data on new taxa within the family and outgroups are necessary to validate this provisional hypothesis.

Coddington (1989) suggests that the viscid glue to the theridiid ss-wrap comes from their enlarged aggregate glands' spigots; since pholcids do not have these structures (their posterior lateral spinnerets are devoid of spigots – see Platnick, Coddington, Forester, & Griswold, 1991), the glue droplets are probably not homologous in these families. Nevertheless pholcids also have a structure similar to the theridiids enlarged aggregate glands, one that could provide large amounts of glue droplets. It is an enlarged piriform spigot, at the anterior lateral spinneret, served by a highly modified piriform gland (Kovoor, 1986) which occurs in all pholcid species and is thus a basal feature in the family (see figs.146-190 in Huber, 2000; fig.133 in Platnick et al., 1991).

The use of distinct, non-homologous silk glands in pholcid and theridiid ss-wrap attack does not imply that the ss-wrap behaviour is not homologous in these families: although distinct, these spigots are serial homologues. Also, the same behavioural performance could rely on distinct structures in distinct families. As an example, mygalomorph and araneomorph spiders all show a quite conservative behavioural sequence while building their silken eggsacs (Japyassú, Macagnan, & Knysak, 2003), despite substantial variations in their spinning apparatus. Careful observations on new spider taxa are necessary to establish the level of generality of these predatory tactics among spiders.

Appendix

Description of behavioural units.

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.

Wrap (Robinson & Olazarri, 1971): after reeling the prey, or after approaching and/or touching it, the spider throws dry silk onto it, with alternate or simultaneous 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. We have not observed the "bobbin like" wrapping that Robinson and Olazarri described for Argiope argentata.

Sticky Silk Wrap Attack (ss-wrap): topologically identical to Wrap (see above). After approaching and/or touching the prey, the spider turns its body 180^0, pointing its spinnerets towards the prey. Next she throws silk with viscid glue towards the prey, with alternate or simultaneous movements of the hind legs (Coddington, 1986).

Wrap attack (Eberhard, 1982): spiders wrap the prey before biting it. This wrapping behavior includes rotating the prey while it is still attached to the web.

Pay-out-line (Japyassú & Caires, *submit.*): after wrapping the prey, at the hanging immobilization phase (see above), the spider moves upward, leaving a line behind. Before moving the spider may fix silk to the prey or to the gumfoot line. This upward movement (without lifting or else carrying the prey on silk) is called Pay-Out-Line. After this the spider fixes once or twice to the gumfoot line, and usually retrieves the prey, i.e, moves down, back to prey. The spider may use this category more than once in the same capture attempt.

Reel (Garcia & Japyassú, *in press*; Japyassú & Caires, *submit.*): the spider hangs upside-down on its sheet, the hind legs grasping the border of the sheet and the anterior legs holding the gumfoot line which detains the prey. She then flexes legs IV quick and strongly, detaching the gumfoot and the prey from the substrate. Next the spider pulls the hanging prey with legs I and II until it gets near enough to be wrapped. Sometimes the prey is already free from the substrate (but not from the gumfoot droplets) when the spider touches the gumfoot line; in these cases, reeling consists simply of pulling the hanging prey with the front legs. The spider may initiate reeling from the border of the sheet, as described above, but may also approach the prey, descending through the gumfoot lines, before reeling. Eberhard (1992a, p. 39) describes *Physocyclus globosus* (Pholcidae) preying on a walking tephritid fly, which seems to be an occurrence of reeling, but the description is not clear enough, and he does not mention the presence of gumfoots. Ades (1972) describes a similar behaviour (lifting, also named retrieve by Japyassú & Viera, 2002). Although topologically similar, these behaviours occur in completely different contexts: reeling occurs before the contact with prey, during the detection phase, and lifting occurs long after prey immobilisation, when the spider is at the retreat or hub and the prey is packed, hanging on a nearby thread.

Manipulate (Robinson & 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.

Bite (Robinson & 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 20s) and short, subtle insertions of chelicerae onto prey (see short bite below).

Short bite: 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 short time (at most 20s - Viera, 1986).

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

Fix Prey (Viera, 1986, 1994): the spider moves her abdomen ventrally, touching the prey (or silk threads around the prey) with the spinnerets, fixes a thread and leaves a new silk strand

Fix (Viera, 1994): the spider moves her abdomen ventrally, touching the web with the spinnerets, fixes a thread and leaves a new silk strand.

Retrieve (Viera, 1994): usually at the resting place, the spider pulls the wrapped package towards her using legs I and II. Theridiids use a similar behavior (see Garcia & Japyassú, *in press*; Japyassú & Caires, *submit.*): usually at the retreat, the spider moves towards the wrapped prey (leaving a line as she moves) which is hanging nearby on a thread or entangled at the periphery of the web.

Carry-on-silk (transp - Robinson & Olazarri, 1971): after the spider fixed 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 & Olazarri, 1971, Robinson & Robinson, 1973) describe another category, carry on jaws, carried out by large spiders usually when preying upon small prey items; this category also occurs among pholcids, but does not seem to occur among theridiids (see Garcia & Japyassú, *in press*; Japyassú & Caires, *submit.*).

Pause (Viera, 1994): the spider halts at any moment of the capture sequence and stands immobile during 30s or more.

Groom (Robinson & 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.

Touch (Robinson & Olazarri, 1971; Viera, 1983, 1986, 1994): the spider simply touches the prey with palps and/or legs (I or II). Usually this occurs after the spider approaches or retrieves the prey. See manipulate above for a similar category.

Tug (Jackson & 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 1-2s then relaxes its legs, returning to the normal position. The spider usually moves towards the prey before tensing the threads with legs I. In the present paper tugging refers not only to the flexing of the first pair of legs, as described by Jackson and Brassington (1987), but also to this quick displacement which sometimes precede this flexion. The spider also tugs consecutively nearby gumfoot lines before reeling (see reel above) one of them.

Abdomen-twitch (ab-twitch - Jackson & Blest, 1982): intermittent movements of the abdomen, dorso-ventrally, 1-4 times (amplitude, *c.* 1mm; duration, *c.* 0.25s).

Bouncy-walk (bouncy - Jackson & Brassington, 1987): special gait in which the spider´s legs are held spread more to the side than usual and leg movements (specially femoral and tibial) are pronounced, causing the spider´s body to move distinctively up and down (2-3mm; *c.* 1/s). The spider appears to bounce along on the silk. Sometimes, she performs boucy walking in place (i.e. without advancing). Sometimes the spider make bouncy movementes while transporting its prey (bw-transp).

Fix and rotate (FixR; Robinson, & Olazarri, 1971; Japyassú & Viera, 2002; Viera, 1994): after fixing the wrapped prey to the retreat, the spider rotate its body sagitally in order to face the prey. While turning, the spinnerets are dabbed against the web in an arc. This sequence of web fixations during the turning process is named FixR. Peters (1931, cited by Robinson & Olazarri, 1971) describes this same movement (which he called Rundgang) for *Araneus diadematus* Clerck, 1757. Japyassú and Viera (2002) calls this category Store. See the discussion for particularities of this choreography in pholcids and araneids.

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