

This article was downloaded by:[University of Pittsburgh]
On: 30 September 2007
Access Details: [subscription number 769430029]
Publisher: Taylor & Francis
Informa Ltd Registered in England and Wales Registered Number: 1072954
Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Natural History

Publication details, including instructions for authors and subscription information:
<http://www.informaworld.com/smpp/title~content=t713192031>

The evolution of prey-wrapping behaviour in spiders

Gilbert Barrantes^a; William G. Eberhard^a

^a Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

Online Publication Date: 01 January 2007

To cite this Article: Barrantes, Gilbert and Eberhard, William G. (2007) 'The evolution of prey-wrapping behaviour in spiders', *Journal of Natural History*, 41:25, 1631 - 1658

To link to this article: DOI: 10.1080/00222930701464364

URL: <http://dx.doi.org/10.1080/00222930701464364>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

The evolution of prey-wrapping behaviour in spiders

GILBERT BARRANTES & WILLIAM G. EBERHARD

Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

(Accepted 21 May 2007)

Abstract

We traced the evolution of silk use by spiders in attacks on prey by combining previous publications with new observations of 31 species in 16 families. Two new prey-wrapping techniques are described. One, in which the spider holds a tense line (often covered with viscid silk) with both legs IV and applies it to the prey with a simultaneous movement of both legs, may be a synapomorphy linking Theridiidae, Nesticidae, and Synotaxidae. The other, in which the spider stands over the prey and turns in place, is apparently very ancient; it occurs in Theraphosidae, Tengellidae, and Agelenidae. The use of legs IV to wrap prey is described for the first time in Filistatidae and Scytodidae. Using a recent phylogeny of spiders, we propose that prey wrapping with legs IV has evolved convergently at least four times. We propose that prey wrapping originally evolved from egg-sac construction behaviour.

Keywords: *Attack behaviour, phylogeny, spiders, wrapping silk*

Introduction

The production of silk lines that emerge from abdominal spinnerets is a defining feature of spiders (Shear et al. 1989), and many spiders use such silk lines to wrap prey (Foelix 1996). There are at least two contexts in which spiders wrap their prey: to restrain active prey so they cannot escape (“immobilization wrapping”); and to form more compact, manageable packages of already immobilized prey to facilitate other activities such as removing it from the web, carrying it, fastening it to the web at the feeding site, or feeding (“post-immobilization wrapping”) (Eberhard 1967; Robinson et al. 1969; Robinson and Mirick 1971; Rovner and Knost 1974; Robinson 1975; Nitzsche 1988). These functions of wrapping are not exclusive, and attack wrapping can also serve post-immobilization functions. The silk that spiders use to wrap prey is presumed to come from aciniform silk glands, although there is little direct evidence (Weng et al. forthcoming); and pholcids wrap prey despite lacking acciniform glands, while ampullate gland silk is probably also used in *Nephila clavipes* (W. Eberhard, unpublished). Possible aciniform gland spigots occur in very ancient fossils (Shear et al. 1989), so prey wrapping may also be very ancient.

Prey-wrapping behaviour has been used as evidence of the relationships between some groups. “Rotisserie” or “prey-rolling” wrapping behaviour, in which the spider pulls a

swath of silk from its spinnerets and wraps it on to the prey by spinning the prey on the line where it is entangled (Peters 1931, 1933; Robinson 1969; Robinson and Olizarri 1971), is a synapomorphy of one subfamily of araneids (Eberhard 1982; Griswold et al. 1998). The use of wrapping silk lines covered with viscid silk, presumably produced by the aggregate glands, is thought to be a synapomorphy linking nesticids, theridiids, and synotaxids (but see below) (Griswold et al. 1998; Agnarsson 2004). Viscid wrapping silk evolved convergently in the distantly related family Pholcidae (Kirchner and Opderbeck 1990). Post-immobilization prey wrapping also occurs, perhaps convergently, in several groups, including among others some lycosids that live above the ground in vegetation (Rovner and Knost 1974), pisaurids (Nitzsche 1988), ctenids (Melchers in Rovner and Knost 1974), drymusids (Valerio 1974), scytodids (Eberhard 1986), and diguetids (Eberhard 1967).

Published descriptions contain few details of the movements of the spider's legs while it wraps prey, other than the common statement that the spider's legs IV make alternate movements to pull wrapping silk lines from the spinnerets and place them on or in the vicinity of the prey. Descriptions are often superficial, however, and the fine temporal resolution available from digital video recordings has apparently never been used before to study the details of wrapping behaviour. We present some behavioural details as "new", but most previous studies cannot be checked for the occurrence of some subtle details, such as the positions of different spinnerets, or the alternate versus simultaneous use of legs IV to apply wrapping silk to the prey. Therefore some of these "new" details may well occur in other species that have been studied previously.

Methods

Responses of spiders to prey were recorded using Sony DCR-VX1000 and Sony DCR TRV50 digital cameras equipped with close-up lenses. The prey used for different species (when noted) are listed in Table I. Prey for the theraphosid were dropped near the spider; prey for the other species were dropped on to the spider's web. In a few cases the prey failed to adhere to the spider's web, so it was first entangled in a bit of cribellum silk from the web of a *Kukulcania hibernalis* (Hentz, 1842) and then the cribellum silk was entangled in the web of the spider. Unless noted otherwise, all spiders were mature females. All means are followed by \pm one standard deviation.

We checked for balls of adhesive material on wrapping lines by placing recently wrapped prey in a small "humid" chamber lined with wet towels for 40 min to several hours, then opening the chamber and quickly observing the lines under a dissecting microscope. This treatment made hydrosopic balls very easy to see. We use the phrase "sticky line" for lines with easily visible balls of liquid on them.

In some recordings some details were not visible, and the sample sizes of different types of behaviour in a given species often varied according to visibility. Details that were not in focus in video images were omitted from drawings based on these images.

Previous studies have shown that in some groups, such as *Argiope*, *Cyrtophora*, *Nephila*, and *Lycosa*, wrapping behaviour varies both qualitatively and quantitatively with circumstances such as the size and taxonomic group of the prey (Robinson et al. 1969; Robinson and Olizarri 1971; Rovner and Knost 1974; Lubin 1980). In this study we were interested in determining whether or not a species could perform a given behaviour pattern, rather than whether or not this behaviour was omitted under certain conditions. We thus tended to use relatively large prey that were difficult for the spider. Some sample sizes are

Table I. Types of prey presented to different species of spiders.

Prey	Spiders
Moths, butterflies	<i>Nephila clavipes</i> , <i>Kapogea sellata</i> , <i>Psalmopoeus reduncus</i> , <i>Tengella radiata</i> , <i>Tortolena</i> sp.
Nematocerus flies	<i>Chryso intervalensis</i> , <i>Helvibis longipes</i> , <i>Philoponella vicina</i> , <i>Ochyrocera</i> sp.
Muscoid flies	<i>Achaearanaa tessellata</i> , <i>A. tepidarium</i> , <i>Anelosimus studiosus</i> , <i>A. pacificus</i> , <i>Azilia affinis</i> , <i>Chryso cambridgei</i> , <i>Gaucelmus calidus</i> , <i>Helvibis longipes</i> , <i>Kapogea</i> sp., <i>Latrodectus geometricus</i> , <i>Nephila clavipes</i> , <i>Nesticoides rufipes</i> , <i>Synotaxus</i> sp., <i>Theridium evexum</i>
Drosophilid flies	<i>Achaearanaa tessellata</i> , <i>Anelosimus studiosus</i> , <i>A. pacificus</i> , <i>Chryso intervalensis</i> , <i>Helvibis longipes</i> , <i>Kukulkania hibernalis</i> , <i>Philoponella vicina</i> , <i>Physocyclus globosus</i> , <i>Theridium evexum</i> , <i>Tortolena</i> sp.
Small acalyptrate flies	<i>Metabus gravidus</i> , <i>Scytodes</i> sp.
Sepsid flies	<i>Achaearanaa tessellata</i> , <i>Alloccyclosa bifurca</i> , <i>Anelosimus pacificus</i> , <i>Physocyclus globosus</i>
Chrysopid	<i>Chryso cambridgei</i>
Roach	<i>Deinopis</i> sp.
Ants	<i>Achaearanaa tessellata</i> , <i>Anelosimus studiosus</i> ^a , <i>Chrosiothes</i> sp. nr. <i>porteri</i> , <i>Kukulkania hibernalis</i> ^b , <i>Scytodes longipes</i> ^c , <i>Theridium evexum</i> , <i>Ochyrocera</i> sp.
Membracid nymphs	<i>Achaearanaa tessellata</i> , <i>Azilia affinis</i>
Cicadellids	<i>Dubiaranea</i> sp., <i>Synotaxus</i> sp., <i>Ochyrocera</i> sp.
Araneid spider	<i>Scytodes longipes</i>
Beetles, wasps, bees ^d	<i>Achaearanaa tessellata</i> , <i>Philoponella vicina</i> , <i>Ochyrocera</i> sp.

^a*Pseudomyrmex* sp. ^bWorkers and soldiers of *Pheidole* sp. ^cWinged male *Camponotus* sp. ^d*Trigona* sp.

small, because once a species was found to execute a particular behaviour in which we were interested, we moved on to another species.

Spiders were identified by the following specialists (in square brackets) and references: *Alloccyclosa bifurca* (McCook, 1887) and *Leucauge mariana* (Taczanowski, 1881) [H. W. Levi]; *Scytodes longipes* Lucas, 1844 (Valerio 1981); *Physocyclus globosus* (Taczanowski, 1874) and *Ochyrocera* sp. [B. Huber]; *Psalmopoeus reduncus* (Karsch, 1880) and *Philoponella vicina* (O. P.-Cambridge, 1899) [B. Opell]; all theridiids, *Synotaxus* sp. and *Gaucelmus calidus* Gertsch, 1971 [I. Agnarsson]; *Dubiaranea* (?) sp. [G. Hormiga]; *Kukulkania hibernalis* (Ubick 2005); *Tengella radiata* (Kulczynski, 1909) (Wolff 1977); *Kapogea* sp. (Levi 1997); and *Azilia affinis* O. P.-Cambridge, 1893 (Levi 1980). *Melpomene* was tentatively identified (generic limits are not clearly defined) by Darrell Ubick. Vouchers have been deposited in the Museo de Zoología of the Universidad de Costa Rica.

Results

Several aspects of wrapping behaviour and sample sizes are summarized in Table II. Descriptions of particular wrapping movements by representative species, and of some unusual details follow. Further details concerning how spiders initiated and terminated wrapping lines, and how they snagged them and then released them with their legs IV will be described elsewhere (W. G. Eberhard and G. Barrantes, in preparation).

Spider pulls wrapping silk by moving its body

Psalmopoeus reduncus (*Theraphosidae*). In each of five taping sessions the spider (a mature female) was fed several living moths that were dropped 1–5 cm from her. Between

Table II. Wrapping behavior of different species of spiders.

Taxon	Immobilization with legs touching ^a	Spinnerets touched with legs IV ^b	Simultaneous (Sim) or alternate (Alt) use of legs IV ^a	Simultaneous use of legs IV more frequent in early wrapping	% of simultaneous movements of legs IV (no. movements, no. prey)	Touch prey with legs IV ^c	Sticky line in early wrapping	At least some video observations	N (prey, spiders)	Spread spinnerets as wrapping	Swath spread with legs IV as applied	Legs or palp (p) used in managing prey	Abdomen swung to side as leg IV grasps line
Theraphosidae													
<i>Psalmopoeus reduncus</i>	No	No	–	–	–	–	No ^d	Yes ^e	>30, 1	Yes	–	–	–
Filistatidae													
<i>Kukulcania hibernalis</i>	No ^f	Yes	Alt	–	–	No	No ^d	Yes ^e	>30, 2	Yes	?	p, I–III	Yes
Pholcidae													
<i>Physocyclus globosus</i>	Yes	?	Alt	–	0 (804, 2)	?	Yes	Yes	>50, >20	Slightly	?	II, III	Yes
Scytodidae													
<i>Scytodes longipes</i>	Yes/no ^g	Yes	Alt	–	0 (512, 1)	Yes	?	Yes	2, 2	Slightly	No	II, III	Yes
Ochyroceratidae													
<i>Ochyrocera</i> sp. ^h	No ⁱ	–	–	–	–	–	–	No	8, 3	–	–	– ^j	–
Agelenidae													
<i>Tortolena</i> sp.	No	No	–	–	–	–	No ^d	Yes	8, 3	Yes	–	–	–
Tengellidae													
<i>Tengella radiata</i>	No	No	–	–	–	–	No ^d	Yes	>20, 2	Yes	–	–	–
Deinopidae													
<i>Deinopis</i> sp.	?	?	Alt ^k	–	–	?	No ^l	No	1, 1	?	?	?	?
Uloboridae													
<i>Philoponella vicina</i>	Yes	No	Alt	–	0 (211 196, 30)	Yes ^m	Yes ^{n,o}	Yes	>50, >10	Yes	Yes	II, III	Yes
Linyphiidae													
<i>Dubiaranea</i> sp.	No	At least close	Alt	–	–	?(Yes?)	?	Yes ^f	4, 4	Yes	?	III ^p	Yes ^q
Theridiidae													
<i>Achaearanea tepidariorum</i>	Yes	?	Sim + Alt	Yes	26 (113, 1)	?	Yes	Yes	1, 1	?	?	?	Yes
<i>Achaearanea tessellata</i>	Yes	?	Sim + Alt	Yes	53 (446, 6)	No	Yes	Yes	>20, >5	Yes	No	II, III ^r	Yes
<i>Anelosimus pacificus</i>	Yes	–	Sim + Alt	Yes	–	–	–	–	10, 1	–	–	–	–
<i>Anelosimus studiosus</i>	Seldom	No ^s	Sim + Alt ^t	No ^u	20 (351, 9)	Yes	Yes	Yes	10, 5	Yes	No	I–III, p ^v	Yes

Downloaded By: [University of Pittsburgh] At: 05:05 30 September 2007

Table II. Continued

Taxon	Immobilization wrapping ^a	Spinnerets touched with legs IV ^b	Simultaneous (Sim) or alternate (Alt) use of legs IV ^a	Simultaneous use of legs IV more frequent in early wrapping	% of simultaneous movements of legs IV (no. movements, no. prey)	Touch prey with legs IV ^c	Sticky line in early wrapping	At least some video observations	<i>N</i> (prey, spiders)	Spread spinnerets as wrapping	Swath spread with legs IV as applied	Legs or palp (p) used in managing prey	Abdomen swung to side as leg IV grasps line
<i>Chrosiothes</i> sp. nr. <i>porteri</i>	Yes	?	Sim + Alt	Yes	–	?	Yes ^w	Yes	3, 3	?	?	–	–
<i>Chryso cambridgei</i>	Yes	–	Sim + Alt	No ^x	43 (748, 2)	No	Yes	Yes	2, 1	Slightly	No	I–III ^y	Slightly ^z
<i>Chryso intervale</i>	Yes	–	Sim + Alt	–	–	–	–	–	5–10, 5–10	–	–	–	–
<i>Helvibis longicauda</i>	Yes	–	Sim + Alt	–	–	–	–	–	5–10, 5–10	–	–	–	–
<i>Latrodectus geometricus</i>	Yes	Close ^{aa}	Sim + Alt	Yes	35 (329, 4)	No ^{bb}	Yes ^{cc}	Yes	9, 4	Yes ^{dd}	Yes	III ^{ee}	Yes
<i>Nesticodes rufipes</i>	Yes	No ^{ff}	Sim + Alt	Yes	31 (189, 2)	Probably no ^{gg}	Yes ^{hh}	Yes	8, 4	Late only ⁱⁱ	Yes ^{jj}	II, III ^{kk}	Yes ^z
<i>Phoroncidia reimoseri</i>	Yes	–	Sim ^{ll} + Alt	–	–	–	Yes ^{mmm}	Yes ^e	2, 2	–	–	–	–
<i>Theridion evexum</i>	Yes	No ⁿⁿ	Sim + Alt	Yes	36 (1087, 8) L; 16 (79, 3) S ^{oo}	No	Yes ^{pp}	Yes	>30, >7	Yes ^{qa}	No ^{rr}	I, III ^{ss}	Yes
<i>Tidarren sisypoides</i>	Yes	?	Sim + Alt	Yes	38 (246, 2)	No	Yes	Yes	4, 2	Yes	No	II, III	–
Araneidae													
<i>Allocclosa bifurca</i>	Yes	No	Alt	–	0 (45, 2)	No	Yes ^{tt}	Yes	>20, >10	?	?	p ^{uu} , II, III	?
<i>Argiope argentata</i>	Yes	No	Alt	–	0 (87, 2)	?	?	Yes	3, 1	Yes	?	p, I, III ^{vv}	Yes
<i>Azilia affinis</i> ^{www}	Yes/no ^{xx}	No	Sim + Alt	Yes	40 (478, 5)	No	?	Yes	5, 3	Yes	Yes	I, III ^{yy}	Yes
<i>Kapogea sellata</i> (?)	No ^k	No	Alt	–	0 (297, 4)	Yes ^{zz}	No	Yes	12, 2	Yes	No	I–III	Yes
Nesticidae													
<i>Gaucelmus calidus</i>	Yes	No ^s	Sim + Alt	Yes	26 (560, 3)	No ^{aaa}	Yes	Yes	>30, 3	Slightly ^{bbb}	Yes	II, III	Yes
Nephilidae													
<i>Nephila clavipes</i>	No	Yes/no	Alt	–	–	Yes ^{ccc}	No	Yes	>30, 5	Yes	Yes	p, II, III	Yes
Tetragnathidae													
<i>Leucauge mariana</i>	No	?	Alt	–	0 (241, 3)	No	?	Yes	4, 3	?	?	I, II, III	Yes
Synotaxidae													
<i>Synotaxus</i> sp. or spp. ^{ddd}	Yes	?	Sim + Alt	?	–	?	No ^{eee}	No ^f	5, 5	?	?	?	?

Table II. Continued

^aWith at least some prey. ^bOr at least very close to the spinnerets. ^cUsually. ^dFrom video images only; lines were not examined in humid chamber. ^eSpider behaviour was slow, and some details were also easily observed with the naked eye. ^fThe spider did not bite some prey before starting to wrap. ^gWrapped only after first immobilizing the prey by spitting on it; sometimes wrapping occurred before, and sometimes after the prey was bitten. ^hSpiders in captivity readily attacked moderate-sized and somewhat dangerous prey by biting, including four cicadellids which were about one-third their size and kicked energetically. They readily approached potentially dangerous prey such as *Solenopsis* ants, but turned away after brief contact with their anterior legs. ⁱLack of attack wrapping in our observations does not convincingly demonstrate that these species do not wrap prey, as it is possible that we did not give them the appropriate prey to elicit wrapping attacks. ^jPrey were seized in the chelicerae, pulled through the sheet web, and not manipulated subsequently. ^kAt least after the first minute or so of wrapping, which was not observed. The description of Robinson and Robinson (1971) also specifies that the leg IV movements of *D. longipes* were in alternation (“bicycling”); since all wrapping movements we saw were quite slow, we suspect their description is correct. ^lLines checked under a dissecting microscope lacked sticky balls. The body of the fully wrapped prey was not compressed, as is typical in uloborids (Eberhard et al. 2006). ^mFrom rapid (500 frames per s) video recordings (R. D. Briceño, personal communication). ⁿNo balls of glue present, but nevertheless at least somewhat sticky (Eberhard et al. 2006). This stickiness is presumably not homologous with that of theridiids and nesticids. ^oSee Weng et al. (forthcoming). ^pOccasionally also palps, legs II. ^qThe coordination with leg movements was variable: in some cases the abdomen moved slightly to the side and posteriorly 0.07–0.1 s after the leg IV passed near the spinnerets; in others the apogee of the lateral movement of the abdomen coincided with the approach of the ipsilateral leg IV; the coordination was still different in others. Wrapping was followed by laying lines that anchored the prey to the sheet in several different directions. ^rSpiders avoided contact with dangerous prey when they initiated wrapping. ^sIn frames of video with best focus legs IV appeared to touch the spinnerets, but not in the frames with best viewing angle. ^tSimultaneous wrapping movements were infrequent, and the spider usually bit prey before wrapping; wrapping nearly always occurred, but was relatively brief. ^uOnly *Pseudomyrmex* sp. ants, of several types of prey offered, were wrapped with sticky silk with simultaneous movements of legs IV. ^vSpider grabbed prey with palps and legs II and III (but seldom I) when biting it. ^wGleaming mass visible in video recordings on or contiguous to prey. ^xThe very first movements were simultaneous, but in the rest of wrapping there was no clear pattern in the relative frequency of simultaneous and alternate movements. ^yLegs I were used with large prey. ^zRhythmic abdominal movements were barely visible. ^{aa}Movements too rapid to be sure about contact, but there were many frames in which it seemed likely. ^{bb}While wrapping with alternate legs IV (and occasionally during simultaneous movements), the leg often touched at least a silk line attached to the prey, if not the prey itself, because the prey was deflected when the leg approached. Even in cases with simultaneous leg movements that did not touch the prey, the line between the legs probably touched the prey or nearby lines, because the prey moved. ^{cc}Very large sticky balls at the very first; in later stages. ^{dd}Probably spread, at least during early wrapping when simultaneous leg IV movements occurred. ^{ee}Legs III held prey during at least last part of wrapping. ^{ff}Lack of contact not absolutely certain: in some sequences it seemed that the tarsus clearly did not touch, but we could not rule out the possibility that intermediate positions were missed in the video record. ^{gg}At least early during wrapping, during simultaneous movements of legs IV that applied sticky silk. ^{hh}Also occasionally later in wrapping attacks. ⁱⁱEarly in wrapping spinnerets were never seen in a spread position; later, during alternate movements of legs IV the spinnerets were clearly spread. ^{jj}Sometimes but not always. ^{kk}Sometimes also palps. ^{ll}Attack behaviour differed from that of other theridiids in that the spider broke and reeled up the line along which she approached the prey (the single, horizontal sticky line, which constituted her entire web). The behaviour following an attack was also unique. The spider again broke and reeled up the line on her way back to her resting site at one end of the horizontal line, and replaced it with a sticky line. When she reached her resting place, she turned 180°, and then reeled in the line behind her (attached to the nearby substrate) with alternate movements of her legs IV. All of these details are identical to the behaviour of *P. studo* (Eberhard 1981). ^{mmm}A thick, bright white line emerged from spinnerets in video recordings. ⁿⁿⁿIn a single video frame with appropriate angle and focus, leg IV did not touch spinnerets. ^{ooo}Large prey (L) were larger than a housefly; small prey (S) were *Drosophila* or mosquitoes. ^{ppp}Viscous glue observed in microscope on lines collected both directly from the spider, and on the wrapped prey. ^{qqq}Widely spread, at least at end of a wrapping bout. ^{rrr}Two thick lines rather than a swath of lines. ^{sss}At beginning of attack legs II and III hold web thread to which prey adheres, later are placed on prey package. ^{ttt}Wrapping lines had small

Table II. Continued

masses of liquid (see Wenz et al. forthcoming), but lacked the large balls typical of theridiids. ^{uu}Prey rotated with legs I, III, and IV; usually spider held web with legs II, but sometimes also held on with one leg II while using the other to rotate the prey. ^{vv}Palps were used when prey was bitten and rotated. ^{ww}Placement of this genus in Araneidae is uncertain (F. Álvarez-Padilla, personal communication). ^{xx}Calliphorid flies prey about the size of the spider were bitten first; smaller membracid nymphs were wrapped first. ^{yy}Legs II and III were only occasionally used to handle prey. ^{zz}Legs IV nearly always contacted the prey during wrapping. ^{aaa}Legs IV may accidentally touch prey as it swings on web thread. ^{bbb}At least at the beginning of the attack. ^{ccc}On the far side of the prey from the spider. ^{ddd}Spiders were observed near Puerto Viejo de Sarapiquí, Heredia, Costa Rica (elevation about 20 m) and at about 800 m in Parque Estadual Intervales, SP, Brazil; they may be different species. ^{eee}Of three prey that were collected after being wrapped, and placed in a humid chamber for 8 h before being observed under a dissecting microscope, one had no lines with droplets, and the others had only one line with a small droplet on it.

two and four moths were fed to the spider in each session; each new moth was dropped only after the previous moth had been subdued and the spider was feeding. Nine attacks were analysed in detail. The spider responded extremely accurately and rapidly to all prey (as quickly as 0.06 s), whether they fell in front, behind, or to her side. The spider even sometimes responded before a falling prey reached the ground. The spider's first response was to turn to face the prey, and lift her front legs; she then struck at the moth with one or both of her front legs. When the prey was more or less in front of the spider, both front legs struck the moth simultaneously. She pulled it toward her, while swiftly moving forward to hold it with her pedipalps and all legs except legs IV until she had grasped it with her chelicerae. Most legs were then placed on the substrate.

When a prey fell to her rear, the spider sometimes struck first with one front leg, then briefly released the prey and reoriented her body to face more nearly toward the prey, and then struck again with both legs I. In one case when the moth fell near the posterior tip of the spider's abdomen, she turned to strike first with her nearest leg III, and then reoriented her body to strike with both front legs. The spider captured prey with up to three moths already in her chelicerae. Only after the struggles of the new prey had subsided as it was held in the spider's chelicerae did wrapping begin.

Wrapping behaviour ($N=12$) that occurred when the spider already had other prey in her chelicerae included up to three stages. In stage I, the spider initiated wrapping lines and attached them to the substrate. She apparently initiated wrapping lines by pressing her long posterior spinnerets briefly to the substrate one or more times (Figure 1a, b). After lifting them barely above the substrate, she swung her abdomen to one side ($34 \pm 18^\circ$, $N=12$), and then to the other ($20 \pm 10^\circ$, $N=3$); these swings were then repeated in four of 10 wrapping sequences, making a short "zig-zag" pattern. During each swing the spider dabbed her posterior spinnerets one to four times to the substrate. Attachments of a band of silk from each posterior spinneret were confirmed in scattered frames of the video recordings, when favourable angles of illumination made the bands visible (Figure 1d, e).

After the last swing, the spider almost always dabbed her spinnerets once or twice as she began the turning movements of stage II. The spider turned in place, rotating around more or less the centre of her cephalothorax, and thus pulling further silk from her spinnerets. During the first part of stage II, she held the prey in her chelicerae, but later she set it down and continued wrapping. The spider began by reversing the direction of turning from the last attachment of stage I, so that her trailing spinneret became the leading one. As she turned, the leading posterior spinneret was directed posteriorly, while the trailing spinneret was raised (Figure 1c). Periodically she dabbed either the leading spinneret or both of them to the substrate. The mean angle she turned between dabs with her leading spinneret was $90 \pm 89^\circ$ (26 dabs in eight sequences); the mean angle between dabs with her trailing spinneret was $151 \pm 265^\circ$ (27 dabs in eight sequences). The spider's abdomen was tilted slightly as she dabbed (Figure 1c), so the outer, lateral portion of the inferior face of the leading spinneret was closest to the substrate. The total angle through which the spider turned during stage II averaged $834 \pm 430^\circ$ ($N=21$). The spider turned an average of $486.0 \pm 388.4^\circ$ while holding the prey, and the rest after setting it down.

Because they were dabbed to the substrate with different frequencies, the leading and trailing posterior spinnerets produced different patterns of lines. When successive attachments were $<180^\circ$ apart (as was particularly common for the leading spinneret), the wrapping lines were laid under tension; but when the spider turned $>180^\circ$ between attachments (particularly common for the trailing spinneret), the band of silk must have become lax (we could not see the lax silk in the video recordings).

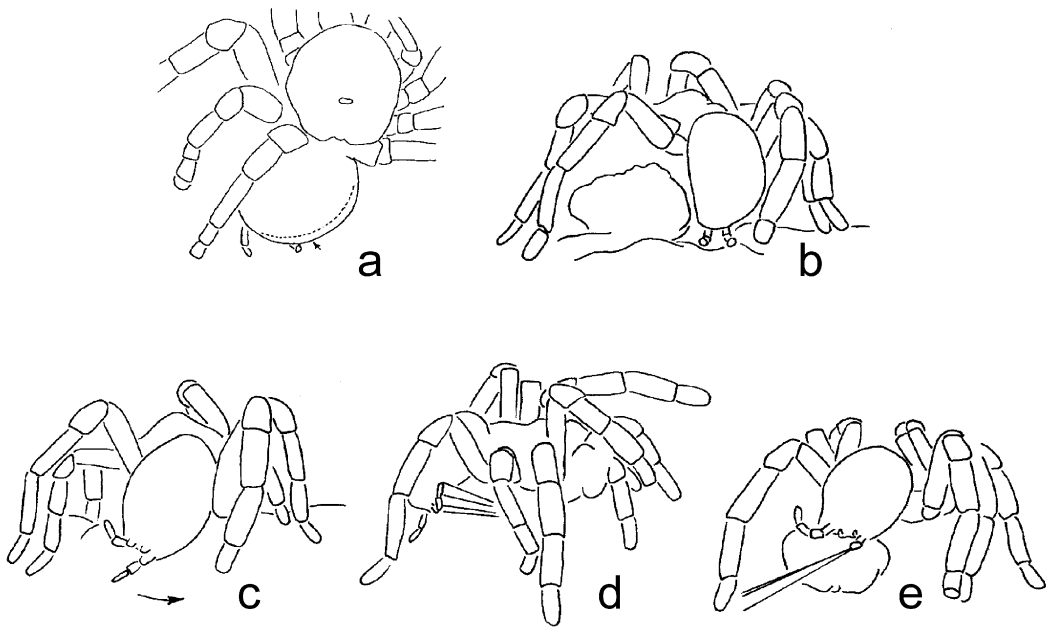


Figure 1. Wrapping behaviour of *Psalmopoeus reduncus* (Theraphosidae). (a) Spider tilts her abdomen to the right as the right posterior spinneret is pressed to the substrate (position indicated by dotted lines followed other position by 0.10 s); (b) the spider presses both posterior spinnerets to the substrate; (c) the spider turns (arrow), swinging its abdomen toward the right while the leading spinneret is lowered and the trailing spinneret is raised; (d) wrapping lines emerging from the trailing, raised spinneret are visible; (e) wrapping lines emerging from the leading, lowered spinneret are visible.

While the spider held the prey in her chelicerae during the first part of stage II, the sides of the prey were wrapped in the lines only when successive attachments were $>180^\circ$ apart, and lines laid between other attachments presumably did not touch the prey. Later, when she placed the prey on the substrate, lines were laid across its upper surface and around it, fastening it loosely to the substrate. The lax silk that accumulated when the angle between successive attachments with the trailing spinneret was $>180^\circ$ may sometimes have been pressed on to the prey by the more frequently attached band from the leading spinneret. It appeared that dabbing both spinnerets at the same time was more frequent as the spider neared the end of stage II.

In wrapping stage III (sometimes after a brief pause while straddling the prey), the spider dabbed both spinnerets to the substrate near the prey two to four times, and then began to lay more zig-zag lines (Figure 2a). Both posterior spinnerets were extended posteriorly, and the spider swung her abdomen laterally, back and forth over the prey as she moved forward. She fastened the bands of silk to the substrate and the surface of the prey with one to four dabs of her spinnerets. Stage III wrapping occurred when the spider had captured at least two relatively large moths (ca 2 cm long) or three or four smaller ones. In other cases the spider started to feed after stage II.

To begin to feed, the spider grasped the bundle in her chelicerae and lifted it; sometimes she also walked several centimetres away. Lifting caused the lines attached to the substrate to be pulled tightly against the top and sides of the prey package, and to break. As the spider fed, she crushed the prey bundle repeatedly with her chelicerae.

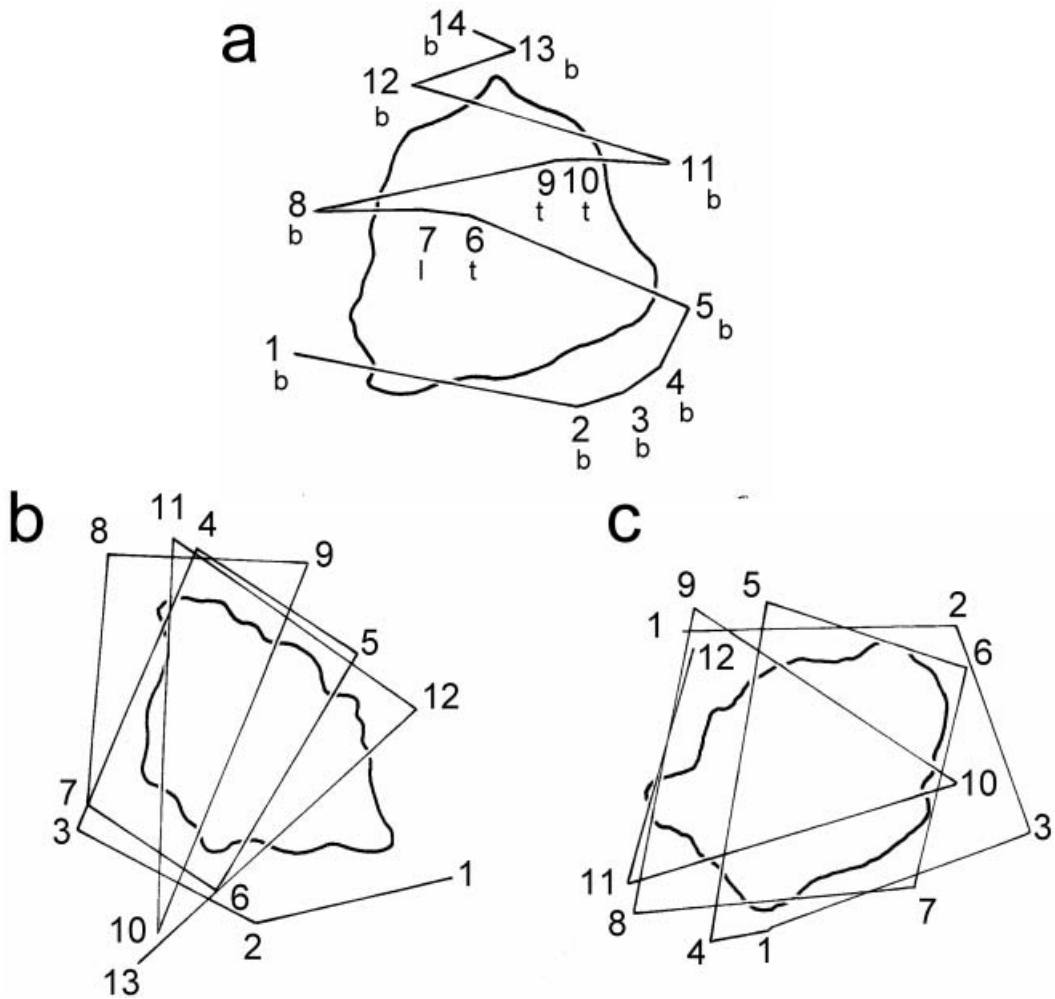


Figure 2. Patterns of attachments of wrapping lines by *Psalmopoeus reduncus* (a) and *Tengella radiata* (b, c) on and near the prey package (thick lines) (numbers refer to order in which attachments were made. (a) Zig-zag attachments by a *P. reduncus* in stage I, prior to turning above a prey (l, attachment by leading spinneret; b, attachment by both spinnerets; t, attachment by trailing spinneret); (b, c) attachments made by *T. radiata* on and near to different prey.

Tengella radiata (*Tengellidae*). Observation of three mature females capturing moths on a sheet web in captivity showed that the wrapping behaviour of *T. radiata* was quite similar to that of *P. reduncus*, despite the fact that its posterior spinnerets are much shorter. This web lacked a retreat, thus facilitating behavioural observations. The spider moved on the upper surface of the sheet at all times. She initiated attacks (eight were recorded on video) by rushing to the prey with her front legs extended anteriorly. As soon as one or both of her legs I contacted the moth, the spider moved rapidly forward, securing the prey with legs I–III against the sheet and her chelicerae. Previously captured prey were left behind as she ran to attack new prey. A minute or so after grasping the prey with her chelicerae, when the prey's struggles had substantially subsided, she began wrapping.

As in stage II of *P. reduncus*, the spider turned in place while attaching wrapping lines to the substrate (the sheet), first while she held the prey in her chelicerae (mean total angle turned = $168 \pm 52^\circ$), and then after she had set the prey down on the sheet (mean total angle turned = $982 \pm 155^\circ$). As she turned, she periodically lowered the tip of her abdomen and dabbed it against the sheet (mean angle between dabs was $94 \pm 39^\circ$, $N=118$ in 12 episodes of wrapping).

While the spider turned, she tapped continuously with her palps on and near the edges of the prey. Occasionally, when lighting angles were favourable, a swath of lines from her posterior spinnerets was visible; their orientations revealed that the swath was attached to the sheet where she had last dabbed the tip of her abdomen. The swath generally passed over the prey a few times (Figure 2b, c). Turning and wrapping prey was seen in only one of about 120 attacks of second instar spiderlings on *Drosophila* sp. prey, and did not become common until approximately the fifth instar.

In all nine different wrapping episodes with good visibility, it was clear that as she turned, the spider's two posterior spinnerets were in the same asymmetrical positions as in *P. reduncus*: the leading posterior spinneret extended posteriorly, while the trailing spinneret was directed dorsally, away from the sheet (Figure 3a). It was not possible to determine whether, as in *P. reduncus*, some attachments to the sheet were made only with the leading spinneret. At least two wrapping lines were visible in some video images (Figure 3b).

If she had left a previous prey when she attacked, the spider usually (seven of eight cases) first wrapped the new prey at the site of capture, and then carried it in her chelicerae, placed it on the first prey, and then wrapped both in a single package.

When the spider finished wrapping, she seized the prey in her chelicerae and lifted it from the sheet, causing the wrapping lines to press on the dorsal and lateral surfaces of the prey package, and break (with little apparent effort). She often carried it a short distance before pausing to feed. In two cases she left the prey and walked several centimetres and pressed her mouth to a piece of a wet sponge for about 30 s (perhaps to take up water so as to be able to feed more effectively?), then returned to feed.

Melpomene sp. (*Agelenidae*). The spider always ($N=10$) left the entrance of the tunnel at the edge of her funnel web to run rapidly across the sheet to the prey, seized it with her chelicerae, and then immediately ran back to the retreat. Within a few seconds she set the prey, which was already nearly immobile, on the sheet at the mouth or 1–2 cm inside the tunnel, and began to wrap it by turning in place while standing over it. She turned a mean of $788 \pm 250^\circ$ ($N=6$) during each burst of wrapping, and performed 1.5 ± 0.6 ($N=4$) bursts of wrapping per prey. Previously captured prey were left behind when she attacked an additional prey, and a new prey was often placed on top of a previous prey at the mouth of the tunnel.

Because of the length of the spider's posterior spinnerets, her rapid jerky movements, and the irregular surface of the outer portion of the tunnel, it was not possible to deduce when she made attached wrapping lines. She initiated wrapping by dabbing against the sheet with her spinnerets and abdomen as in *Psalmopoeus* and *Tengella*, but later in wrapping dabbed only irregularly. In some cases, however, it was clear that the leading posterior spinneret was lowered and the trailing posterior spinneret was raised while the spider turned in place (Figure 3c). When wrapping ended, the raised spinneret was lowered.

During most wrapping behaviour the spider stood over or very near the prey as she turned. In a few cases, however, in all of which she had already captured several other prey, the spider disappeared down the tunnel for several seconds, and then reappeared to continue turning in place.

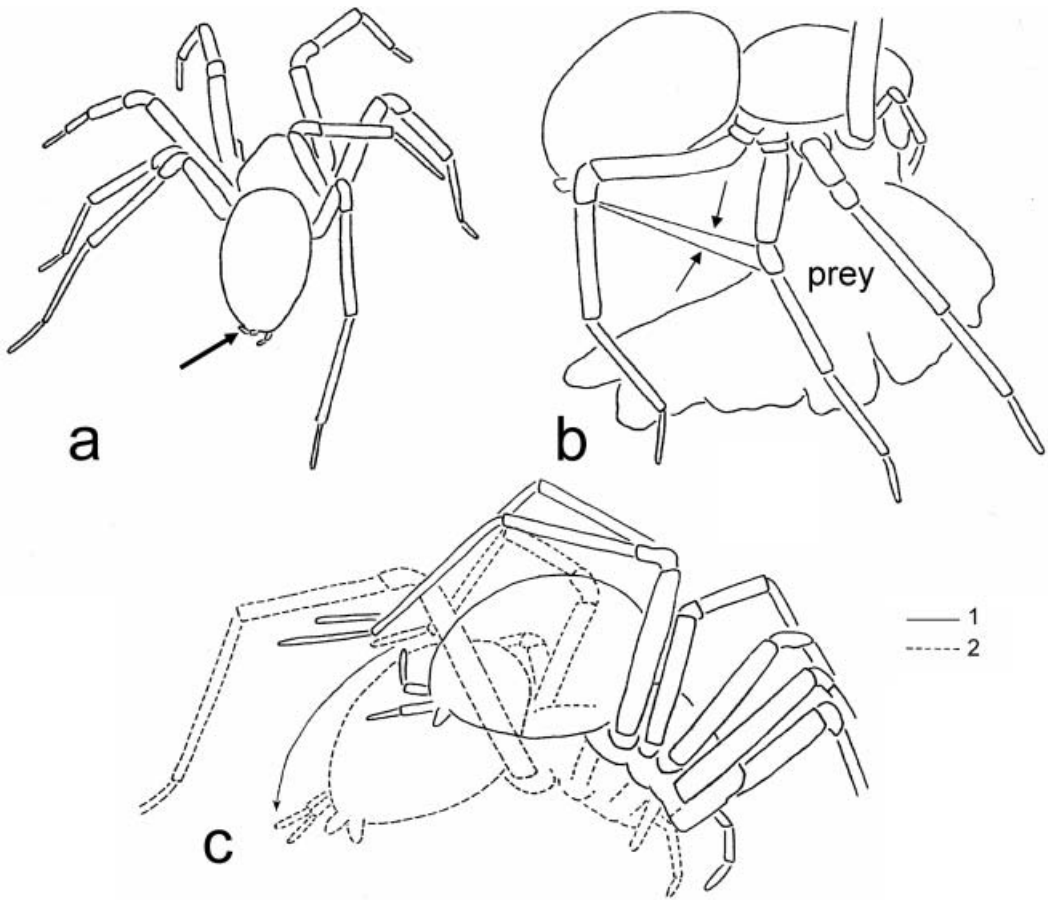


Figure 3. Wrapping behaviour of *Tengella radiata* (Tengellidae) (a, b) and *Torolena* sp. (c). (a) The trailing spinneret was raised (arrow) while the leading spinneret was lowered; (b) a pair of lines from the spinnerets (arrows) were visible; (c) the spider turns while standing over the prey (not shown), with the leading spinneret lowered and the trailing spinneret raised. The time elapsed between the positions indicated with solid and dashed lines was 0.50 s.

Wrapping with alternate movements of legs IV

Kukulcania hibernalis (Filistatidae). One moderate-sized nymph and a mature female were taped. There were no perceptible differences between wrapping movements used with the different prey, though *Pheidole* sp. ants were wrapped more extensively. In nearly all cases the spider walked or ran to the prey and seized it with its chelicerae. Then, within a few seconds and apparently without shifting its hold on the prey, the spider began to wrap it. In one attack on a soldier ant, however, the spider wrapped briefly before biting; it turned and made several wrapping movements with its hind legs before grasping the prey with its chelicerae, pushing wrapping silk to the web on either side of the ant. In three other attacks on soldier ants, the first bite was very short (or perhaps did not occur): the prey was quickly pulled toward the spider and immediately released (as little as 0.07 s later), and then wrapped. This species thus performed only post-immobilization wrapping for most prey, but in a few cases also used wrapping at least briefly to initiate immobilization.

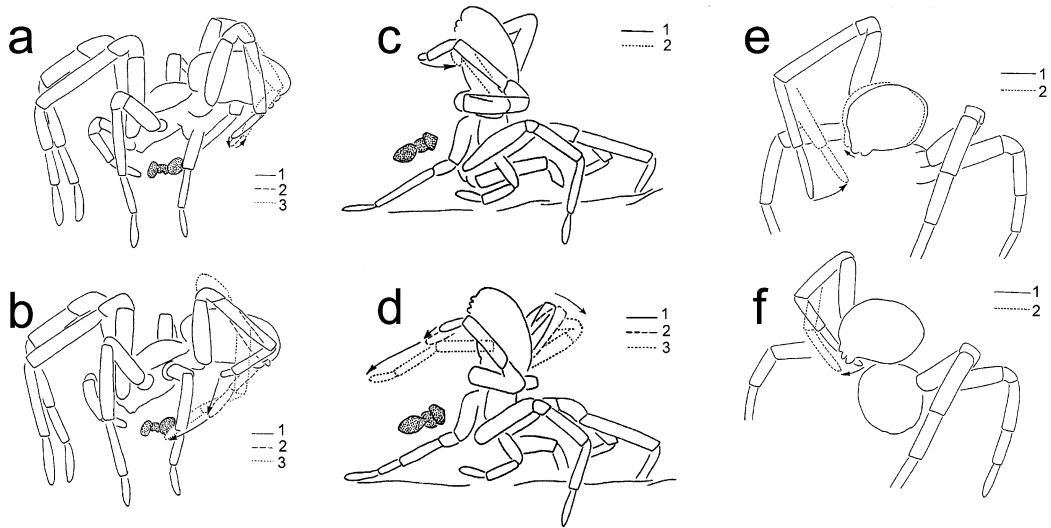


Figure 4. Wrapping behaviour by the filistatid *Kukulcania hibernalis*. (a, b) In lateral view, the spider pulls wrapping lines from the spinnerets with its left leg IV (a) and then pushes them toward the prey (b); (c, d) a lateral view of a similar sequence, but in which the spider's spread spinnerets are visible and its body is lifted about 90°; the right leg IV pushes silk toward the prey while the left leg IV withdraws from the prey and prepares to pull more wrapping silk from the spinnerets; (e, f) in a posterior view, the spider twists its abdomen toward the left leg IV (e) as this leg is brought near the spinnerets and begins to pull wrapping lines (f). The time elapsed between lines labelled 1, 2, and 3: 0.03 and 0.03 s (a), 0.03 and 0.10 s (b), 0.03 s (c), 0.03 and 0.17 s (d), 0.07 s (e), and 0.03 s (f).

To wrap, the spider usually raised its abdomen from the substrate by inclining its body steeply (Figure 4a–d), spread its spinnerets, and apparently pulled lines from its spinnerets with (usually) alternate, moderately slow strokes of its legs IV (Figure 4d). Wrapping lines were apparently thin and sparse, as they were seldom visible in the video recordings; their probable positions were deduced from the positions of the spider's legs. The most rapid movement of the leg was the ventral movement near the spinnerets, lasting only about 0.03 s; the tarsus, which had crossed the midline of the abdomen, moved sharply prolaterally, pulling away from the spinnerets. For each stroke, the abdomen was generally inclined laterally toward the side of the hind leg that would be used. The tarsus or the metatarsus of this leg passed near the spinnerets, and may well have contacted them in some cases, but not in others. It then moved ventrally and anteriorly to the vicinity of the prey, and then moved rearward again. Some wrapping movements appeared clumsy, and the spider sometimes lurched posteriorly, apparently for lack of a posterior brace (both legs IV were wrapping).

After having wrapped the prey, the spider pulled it from the web, sometimes clearly cutting lines by bringing them to its mouthparts. In other cases, it simply lifted the prey, pulling a cone of silk away from the sheet as it did so (it was not clear whether these were wrapping lines or cribellate silk from the web). Without further manipulation of the prey, it moved toward its retreat, usually walking backward. Wrapped prey were not very compressed, and their legs and antennae often still protruded. When attacking a subsequent prey, the spider usually left the previous prey behind in the retreat.

Physocyclus globosus (*Pholcidae*). The spider began attacks by applying wrapping silk with rapid, alternate movements of legs IV; her abdomen swung and inclined from side to side in

close coordination with these movements. Later the prey was freed from the web, and wrapping lines were applied while it was rotated (the direction of rotation was not consistent). The spider's movements were rapid, and difficult to follow. One difference with respect to all other species was that legs III often tapped the prey, sometimes extensively, just before wrapping began. The first lines applied to the prey were covered with glue (Figure 5), but later lines appeared to lack glue. There were "serrated bristles" on the tarsus IV somewhat similar to those of *P. phalangioides* (Kirchner and Opderbeck 1990) and theridiids (Agnarsson 2004) that are probably associated with sticky wrapping silk (W. G. Eberhard and G. Barrantes, in preparation).

Scytodes longipes (*Scytodidae*). Initial immobilization was never accomplished by wrapping, but rather by spitting sticky silk on to the prey. Some prey were then wrapped, while others were first bitten and then wrapped. Wrapping involved relatively slow, alternate movements of legs IV. Wrapping lines were only seldom visible in the video records. We did not check prey for sticky wrapping lines, as we would not have been able to distinguish them from the spitting silk.

Philoponella vicina (*Uloboridae*). The wrapping behaviour of *P. vicina* is described in detail elsewhere (Eberhard et al. 2006; Weng et al. forthcoming). From the beginning of each attack, legs IV moved in strict alternation and in coordination with side-to-side movements of the abdomen. Lines of wrapping silk were somewhat adhesive, but were smooth, without any sign of any additional viscous material when observed under the scanning electron microscope (Eberhard et al. 2006).

Alloccyclosa bifurca (*Araneidae*). The spider approached the prey along the radius in her orb web on which the prey rested. The wrapping lines were apparently initiated when she attached her dragline to this radius, and emerged as a swath when she swung her abdomen

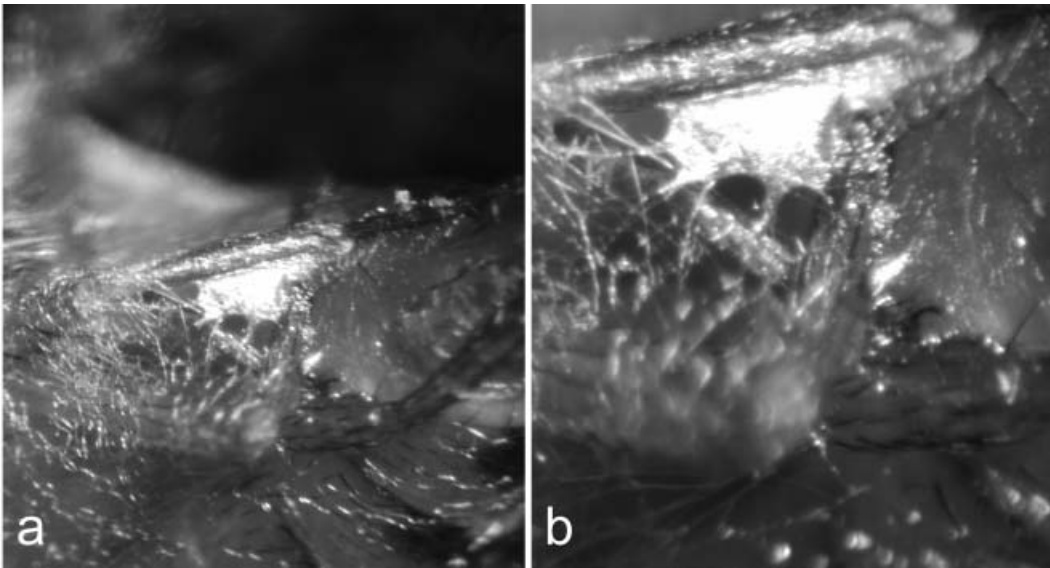


Figure 5. (a, b) Portions of a *Drosophila* fly that had been wrapped by the pholcid *Physocyclus globosus* were covered with a film of apparently liquid, presumably gluey substance; (b) close-up.

laterally to begin wrapping. Silk was laid on to the prey with alternate movements of legs IV, and also when she rotated the prey “rotisserie” fashion on one or more radii with her anterior legs, thus pulling a swath of wrapping lines directly from her spinnerets without touching these lines with her legs (see Robinson and Olizarri 1971, Robinson et al. 1971, Robinson and Robinson 1974, and Eberhard 1982 for similar behaviour in other araneines). The direction of rotation was consistent: the upper side of the prey rotated toward the spider, and the lower side (where the wrapping lines were applied) away from her. Large amounts of silk were applied rapidly, and the prey was soon covered with a thick, opaque sheet of white silk. Examination under the electron microscope revealed drops of liquid on these lines that were not visible to the naked eye (Weng et al. forthcoming).

Nephila clavipes (Linnaeus, 1767) (*Nephilidae*). All our observations were compatible with previous descriptions of the behaviour of this species (Robinson et al. 1969; Robinson and Mirick 1971) and the related *N. maculata* (Robinson and Robinson 1973). Wrapping occurred only after the prey had been subdued by being bitten. Wrapping lines were sometimes initiated on the dragline. After initiating wrapping while the prey adhered to the lines of the orb, the spider gradually freed it by either pushing the web ventrally away from the prey as she held it in her chelicerae, or by cutting these lines. After the prey came free, it was often slowly rotated by the palps and legs II and III while legs IV laid silk on to it with alternate movements (legs I held the orb and sustained the spider). The direction of rotation was not consistent.

Dubiaranea (?) sp. (*Linyphiidae*). As in *Linyphia marginata* (Koch) (Eberhard 1967), all attacks began with a long bite, after the spider had run rapidly to the prey. The bite lasted a minute or more, until the prey's struggles subsided. In some cases the spider then removed the prey from the sheet by pushing the sheet ventrally with her legs while holding the prey in her chelicerae (as in *Nephila*), or cut it free from the sheet, while in still others she wrapped the prey, either while it was in the sheet, or after having freed it. Her legs IV moved relatively slowly, making alternate anterior movements that carried silk from her spinnerets to lay it on to or near the prey. Brief bursts of wrapping alternated with short excursions one to two body lengths away from the prey to attach an “anchor” line from the prey to the sheet, then back to attach her drag line to the prey. After making about 5–10 such anchor lines to the sheet, the spider began to feed, leaving the prey where she had anchored it.

Simultaneous wrapping with legs IV

Theridion evexum Keyserling, 1884 (*Theridiidae*). The behaviour of this slow-moving species will be described in detail, as it can serve as a point of reference for that of others in the family Theridiidae. Some wrapping attacks began using a line which had visible balls of a clear liquid on it (presumably from the aggregate gland), and included simultaneous application of wrapping line to the prey with both legs IV at once, a behaviour that has not been described previously. The attack on a muscid fly depicted in Figure 6 is typical. The spider slowly approached the prey, which adhered to a long vertical sticky line. She touched the prey one or more times with one leg I, then withdrew this leg (Figure 6a) and turned 180° (Figure 6b, c) to begin wrapping. Early in the turn the spider attached her drag line to the vertical sticky line to which the prey adhered (Figure 6b). At the moment of attachment, she probably held this line on either side of the attachment point with the tarsi of her legs III and IV. She then reached rearward (upward arrow in Figure 6b) and seized this vertical line

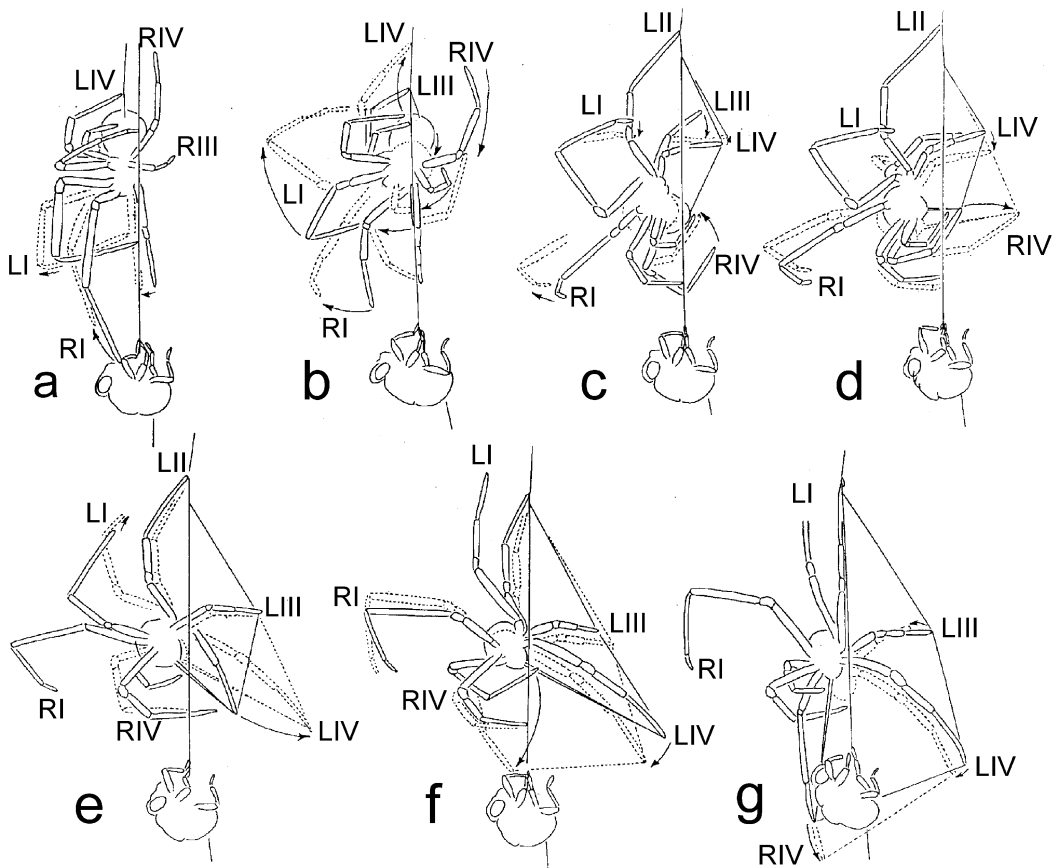


Figure 6. Early stages of an attack on a fly prey by *Theridion evexum*. (a) The spider tapped prey with her right leg I and quickly withdrew it. Then she turned to face away from the prey (b–e). She attached her drag line to the line along which she had been descending (b), and reached posteriorly with leg II to grasp the line above (b, c). She seized her drag line with her left leg III (c), and also brought her right leg IV to her spinnerets (c) to begin to pull what may have been the first segment of sticky wrapping line (c, d). She then pulled additional segments of wrapping line with her left leg IV (e) and right leg IV (f). Finally, she applied the line between the two legs IV to the prey with a simultaneous ventral movement of both legs IV (g) (small arrows show movement between positions indicated by the solid and dotted lines). The time elapsed between first and second positions was 0.27 s (a), 0.24 s (b), 0.12 s (c), 12 s (d), 0.12 s (e), 0.07 s (f), and 0.03 s (g).

with one leg II (Figure 6c), a hold that she would use to support herself for the rest of the wrapping sequence. She also pushed the drag line away from her body with one leg III (Figure 6c, d), brought one tarsus IV to her spinnerets (Figure 6c), and pulled out a length of sticky wrapping line (longest arrow in Figure 6d). This line included at least two fibres (Figure 6e, f), and bore visible balls of glue. Before moving this leg IV toward the prey, she seized the wrapping line with her other tarsus IV near her spinnerets (Figure 6f) and pulled out an additional length of sticky line (Figure 6f, g). When this pulling movement was complete (solid lines in Figure 6g), there was a tight segment of sticky wrapping line between the two extended tarsi IV (dotted lines Figure 6f). The two legs IV then moved simultaneously toward the prey (Figure 6g), and pressed the tight segment of wrapping line against the prey. Her legs IV continued the ventral-medial movement, sometimes pressing the line against the sides and even on to the far surface of the prey. Legs IV then returned to

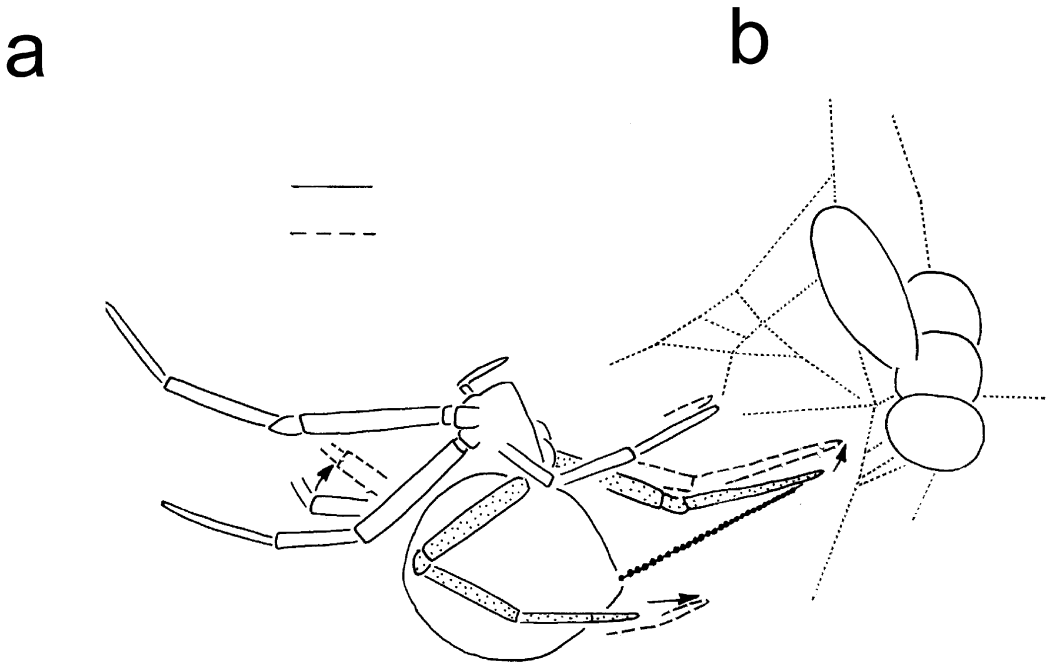


Figure 7. Stages in simultaneous use of legs IV early attack behaviour by *Nesticoides ruficeps* on a muscoid fly. (a) The left leg IV pulled a segment of sticky wrapping line from the spinnerets (dotted black line). This leg then held the sticky line (solid lines in (b)) while the right leg IV pulled an additional length of sticky line, and then both legs IV swung ventrally and anteriorly to apply the sticky line to the prey (dotted lines in (b)). The time elapsed between positions indicated by solid and dotted lines was 0.03 s (a) and 0.07 s (b).

seize and apply further segments of wrapping line to the prey. In the later stages of wrapping, the spider applied lines that were probably not sticky, and most leg IV wrapping movements were in alternation rather than simultaneous.

Nesticoides rufipes (Lucas, 1846) (*Theridiidae*). After approaching the prey and touching it with her front legs, the spider turned to face away, and applied sticky wrapping line with repeated simultaneous movements of her legs IV as in *T. evexum* (Figure 7). The position of the drag line as the spider turned prior to wrapping was not clear in the videos. Sticky wrapping lines were applied for an unusually long time (up to 43 s) before non-sticky lines were applied.

Achaearanea tessellata (Keyserling, 1884) and *Chrosiothes sp. nr. porteri* (*Theridiidae*). The context in which attacks by these two species occurred was quite different from those of other theridiids, because both species construct a dense horizontal sheet in their webs (Eberhard et al. forthcoming), and the sheet formed a barrier between the spider and her prey. The prey was generally on the upper surface of the sheet, while the spider ran rapidly on the lower surface of the sheet to attack it. Nevertheless, both species initiated attacks by wrapping with lines heavily laden with liquid (easily noted with the naked eye); these lines generally held the prey in place on the sheet. In both species the sticky wrapping line was applied using both simultaneous and alternate movements of legs IV. After the prey had been partially restrained, the spider gradually cut the nearby lines of the sheet while she

continued to wrap, thus giving her wrapping lines greater access to the prey. In the later stages of attacks, spiders of both species appeared to use thinner, multiple wrapping lines that lacked any obvious liquid, and also tended to utilize alternate leg IV movements more frequently.

Anelosimus studiosus (Hentz, 1850) (Theridiidae). Mature females of the solitary *A. studiosus* attacked many muscid and drosophilid flies by biting, and only wrapped them with dry silk following the bite, using alternating movements of legs IV. Sticky wrapping silk was used prior to biting only in attacks on *Pseudomyrmex* ants, and was applied with simultaneous movements of legs IV. The spiders appeared to treat these ants with great caution.

A. pacificus Levi, 1956 (Theridiidae). In contrast to the reluctance of *A. studiosus* to utilize sticky silk and immobilization wrapping, *A. pacificus* consistently used both. Their attacks on flies usually began with wrapping rather than biting, and the early stages consistently included sticky silk and simultaneous movements of legs IV. Later in an attack, the spider shifted to applying non-sticky silk and often used alternate movements of legs IV.

Phoroncidia reimoseri Levi, 1964 (Theridiidae). The web of this species consisted of a single sticky horizontal line, and the spider rested at one end of this line. In one videotaped sequence, her first wrapping line was apparently sticky, and was applied with simultaneous movements of legs IV. Direct observations of a second spider were in accord with these observations. Attack behaviour differed from that of other theridiids in that the spider broke and reeled up the horizontal line along which she approached the prey, and then broke and reeled up this line again on her way back to her resting place; on the return trip, she replaced the line with new sticky line. When she reached her resting place she turned 180°, and reeled in the line behind her with alternate movements of her legs IV. All of these details were identical to the behaviour of *P. studo* (Eberhard 1981).

Gaucelmus calidus Gertsch, 1971 (Nesticidae). The uncertainty regarding the phylogenetic relations between Nesticidae and Theridiidae (Agnarsson 2004; Arnedo et al. 2004) justify a more detailed description of the behaviour of this species. The spiders built webs with relatively large amounts of sticky material that covered most of the long vertical capture lines (Eberhard et al. forthcoming). Two attacks were filmed using infrared light (which provided occasional images of the silk lines), and five others under daylight illumination. The spider approached the prey slowly, tapping ahead with her long legs I. After touching the prey, she turned approximately 180°, and pulled a sticky silk line from her spinnerets with a stroke of each of her legs IV (dotted lines in Figure 8a), and then rapidly moved these legs simultaneously so that the line was pressed against the bottom or sides of the prey bundle (dotted lines in Figure 8b). This line gleamed, suggesting that it probably carried sticky balls. This suggestion was confirmed by examining the lines on three prey that were taken from the spider soon after an attack was initiated and checked under a microscope; many lines were covered with moderately small balls of viscid silk.

The spider then applied additional wrapping silk, at first mostly using simultaneous applications with the legs IV, but gradually using alternate movements of legs IV more frequently. These lines were less consistently visible in the videos, suggesting that they may not have been covered with viscid material. The wrapping movements of the legs IV during

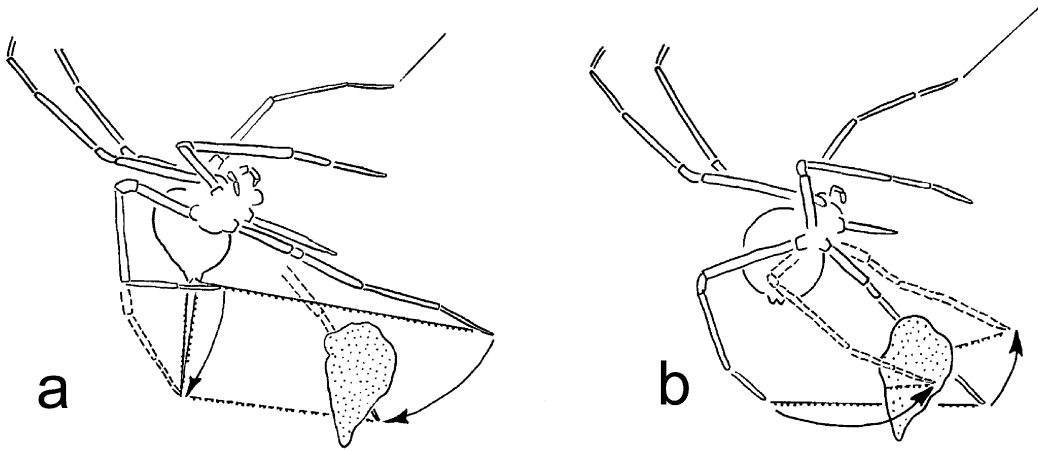


Figure 8. Antero-lateral view of simultaneous wrapping movements of legs IV of a mature female *Gaucelmus calidus*. The spider first pulled sticky silk (with small black dots in drawing) from her spread spinnerets (second leg IV pulls line in dotted lines of (a)), and then moved both legs IV past the prey, snagging the sticky line between them on the prey (dotted lines in (b)). The time elapsed between positions indicated by solid and dotted lines was 0.1 s in both drawings.

this stage were unusual in that the tip of the tarsus moved only barely across the midline of the spider and grasped the line near the spinnerets.

The prey was not turned while being wrapped. Many wrapping movements of legs IV applied the silk to the far side of the prey from the spider, and tarsus IV sometimes even crossed its midline, thus apparently wrapping lines around the sides and the far side of the prey package. The prey was not bitten until after up to 45 s of wrapping, often after the spider had moved away upward toward her retreat and then returned. The prey was carried to the retreat in the upper tangle of the web before feeding began.

Just before feeding, the spider sometimes descended to the substrate and attached a line which may have been a new capture thread. In at least one case, the distal portion of this line was unusually shiny and apparently covered with viscid silk.

Synotaxus sp. (Synotaxidae). The spider approached the prey slowly, tapping with her legs I, and initiated the attack by turning approximately 180° and applying silk to the prey simultaneously with both legs IV. The movements were slow enough to afford a good view of the wrapping lines, which did not appear to have balls of liquid on them. Examination of three wrapped prey packages under a microscope after being in a humid box confirmed this: one entirely lacked sticky balls, and the other two each had only a single tiny ball.

Azilia affinis (Araneidae). Spiders attacked by wrapping rapidly with a thick swath of lines that quickly coated the prey in white. The lines did not seem to have glue on them, and lines in a humid chamber had only very small, scattered droplets. Simultaneous wrapping movements of legs IV, which applied a swath of lines under tension between the two tarsi IV to the prey (Figure 9), were clear and common. The swath often widened at the point where the hind tarsus contacted it, and thus was not gripped by a single structure on the leg.

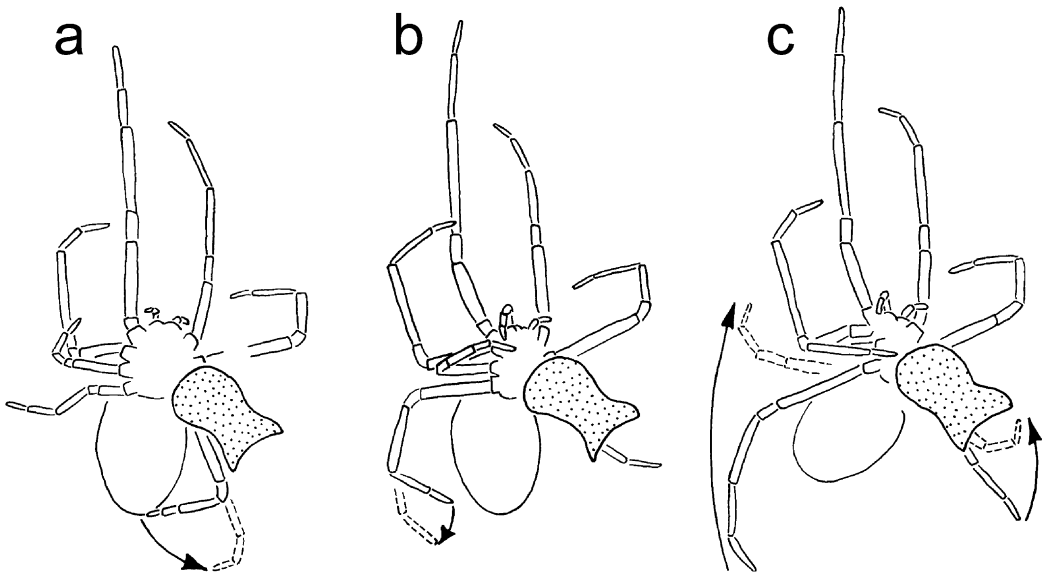


Figure 9. Ventral view of simultaneous wrapping movements of a mature female *Azilia affinis* wrapping a prey (stippled) (view from above the horizontal orb). First one (a) and then the other (b) leg IV pulled silk from the spinnerets, and then both legs were moved simultaneously ventrally (arrows in (c)) to press the line between them against the prey. The time elapsed between positions indicated by solid and dotted lines was 0.10 s (a), 0.10 s (b), and 0.03 s (c).

Discussion

Behavioural details and functions

The wrapping movements of *P. reduncus*, *T. radiata*, and *Melpomene* sp. were similar in that the prey was fastened to the substrate after being bitten and immobilized. Silk was pulled from the posterior lateral (PL) spinnerets by dabbing the spinnerets and the abdomen to make an attachment to the substrate and then pulling away, rather than by pulling lines from the spinnerets with legs IV as in the other species we observed. The most striking similarity among these three species was that the posterior lateral spinnerets assumed similar, asymmetrical positions. One PL was lowered and produced a more or less tightly stretched swath of silk as it repeatedly dabbed the substrate while the spider turned in place. The other spinneret was raised, and at least in the theraphosid, where we were able to observe more details, the raised spinneret produced a more lax swath of silk. Wrapping apparently functions to anchor the prey to the substrate or to compact it (especially as it was lifted away from the wrapping site), and thus perhaps facilitates transport or feeding (and in the theraphosid, wrapping may also facilitate subsequent attacks when the prey remained in the chelicerae). Lycosids (Rovner and Knost 1974) and pisuarids (Nitzsche 1988) also fasten prey to the substrate, but the positions of their spinnerets during this behaviour are unknown.

The theraphosid differed from the other two species in two basic respects. First, during the first part of stage II of wrapping, the spider did not release the prey from her chelicerae. As she turned, she thus moved the prey into the mass of lax wrapping silk produced by her dorsally directed spinneret, rather than relying on the turning movements of her body to stretch wrapping silk across the prey. Another difference was the regular zig-zag

attachments to the substrate when wrapping began (Figure 2a). The other two species never made this type of movement, perhaps because their piriform glands produce more secure attachments (see Coddington 2005).

In the other species, which used their legs IV to draw silk from their spinnerets to wrap prey, legs IV usually moved in strict alternation. Simultaneous leg IV movements to apply wrapping silk to the prey reliably occurred, however, in theridiids and the closely related nesticid and synotaxid species during the initial stages of wrapping. Simultaneous application has at least two possible functions. The wrapping lines were tight when they were applied to the prey, and may have provided more effective, tighter restraint compared with the more lax lines that are sometimes pushed toward the prey by alternating movements of legs IV. Simultaneous application of wrapping lines with both legs IV probably also facilitates extricating the tarsi from each new segment of wrapping silk after it has been applied to the prey, as the two tarsi could pull against one another. Facilitation of removal of the leg from the line could even occur when the wrapping line fell short of the prey. Some spiders have frequent problems removing their tarsi from wrapping lines (W. G. Eberhard and G. Barrantes, in preparation). Removal of the tarsus from the sticky wrapping silk of theridiids may be particularly difficult. Both the restraining and the extraction functions are more likely to be important early in an attack, when simultaneous movements of legs IV tended to occur. In contrast, the bundling function does not require especially tight restraint to overcome prey struggles (Eberhard et al. 2006).

Several species, including the theridiids *Theridium* and *Nesticoides*, the nesticid *Gaucelmus*, and the uloborid *Philoponella*, showed caution by initiating wrapping attacks when the spider was still slightly out of range of the prey. This caution suggests that the advantage of beginning wrapping attacks while at a safe distance is probably important.

The association between simultaneous wrapping movements and sticky wrapping lines was not strict. Simultaneous applications with legs IV were especially common early in wrapping when theridiids and the nesticid were applying wrapping lines covered with glue. But they also occurred later, when thinner lines without obvious balls of glue (presumably from aciniform glands) were being applied to the prey. In addition, they occurred in the synotaxid *Synotaxus* sp. and the araneid *Azilia affinis*, in which sticky lines were sparse or absent.

Evolutionary hypotheses

Several evolutionary hypotheses suggested by our observations are illustrated in Figure 10, using a recent hypothesis concerning the phylogenetic relations among spider families (Coddington 2005). Most families are omitted for lack of data, and this figure obviously represents a speculative guide for future work rather than a definitive conclusion. Because we believe that selective values of traits probably play important roles in their evolution, some of our hypotheses are not “orthodox” in the sense of not being the most parsimonious with respect to the numbers of transitions. The hypotheses and some alternatives are discussed below.

Egg-sac construction and the origin of prey wrapping

One possible evolutionary origin of wrapping behaviour is egg-sac construction. It appears that all or nearly all spiders construct a silk covering for eggs (Foelix 1996), and several authors have argued that silk lines (a synapomorphy for spiders) originally functioned to

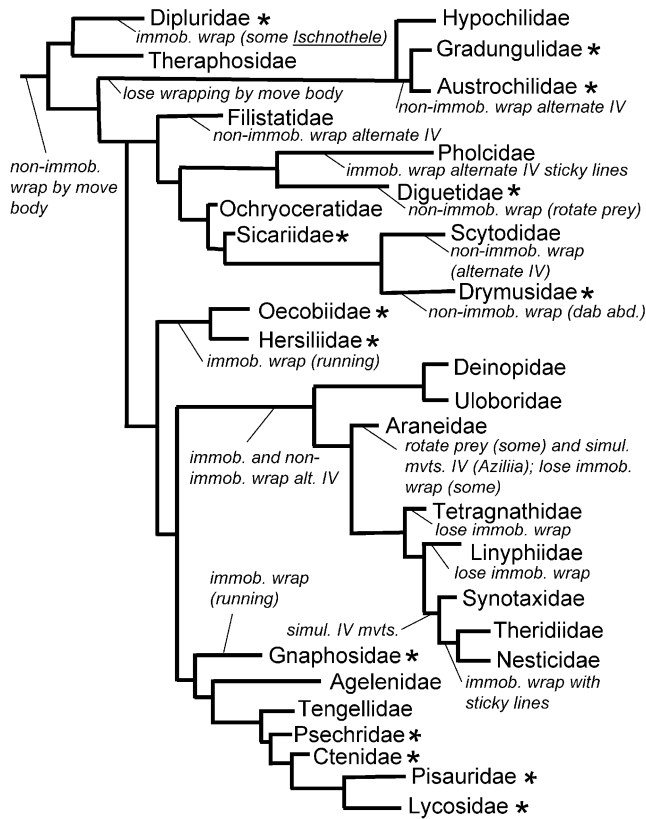


Figure 10. Hypotheses regarding the evolution of several prey-wrapping behavioural characters, including wrapping by moving the body versus moving legs IV, non-immobilization wrapping versus immobilization wrapping, alternate versus simultaneous movements of legs IV, and wrapping the prey by rotating it on the web line on which it was snared. The hypotheses are illustrated by super-position of the behaviour of the groups observed directly in this study or in previous publications (*) on a tentative phylogenetic tree (modified from Coddington 2005). Justifications of the hypotheses are discussed in the text.

cover eggs (Kaston 1964). Egg-sac construction is probably an extremely ancient trait in spiders. The behaviour patterns used in the egg-sac construction of some species are similar to wrapping behaviour without using legs IV that we describe above. Both drawing and applying lines using dabbing movements of the spinnerets and the abdomen, and spreading the spinnerets apart so that the spigots are probably brought into contact with the substrate, occur during egg-sac construction in several species, and occur in groups in which spiders manipulate lines with their legs IV in other contexts. These include the araneids *Cyrtophora citricola* (Forskål, 1775) (Kullmann 1961), *Araneus quadratus* (Getaz, 1889) (Crome 1956), *Mastophora dizzydeani* Eberhard, 1981 (Eberhard 1980b), and *Metazygia* prob. *wittfeldae* (McCook, 1894) (G. Barrantes, unpublished), and the uloborid *Uloborus trilineatus* (?) Keyserling, 1883 (W. Eberhard, unpublished). Species in other groups such as the clubionid *Agroeca brunnea* (Blackwall, 1833) (Holm 1940), the sicariid *Loxosceles intermedia* Mello-Leitão, 1934 (Fischer and Vasconcellos-Neto 2005), and the pisaurid *Paratrachelea* (= *Trachelea*) *ornata* (Mello-Leitão, 1943) (L. E. Costa Schmidt, personal communication) also build egg sacs by dabbing the abdomen to the substrate. On the basis of the widespread

occurrence in spiders of egg sacs made of silk that emerge from the spinnerets when they are dabbed to the substrate, we propose that the wrapping movements of *P. reduncus*, *T. radiata*, and *Melpomene* sp. described here were derived from egg sac construction behaviour. An alternative, similarly ancient source of silk, the sperm web that is produced by the epiandrous glands and their spigots, seems less likely because all known wrapping silk comes from the spinnerets rather than the epiandrous glands.

Pull wrapping silk using movements of the body. On the basis of its simplicity (in terms of the number of behavioural capabilities), its occurrence in mygalomorph spiders, its occurrence during the post-immobilization wrapping behaviour of several other spider families, and its resemblance to egg-sac construction behaviour, we propose that prey wrapping by moving the entire body and the spinnerets, without using the hind legs to manipulate silk, is ancestral in araneomorph spiders. The homology of non-immobilization wrapping in mygalomorph, tenebrionid, and agelenid spiders, as opposed to independent derivations, is supported by the similarity in their asymmetrical use of PL spinnerets. Such asymmetry alters the distribution of lines on the prey package from that expected if the spinnerets were used symmetrically; but the likely selective consequences of such distributions seem so small that it strains credulity to suppose that this similarity between the two groups arose due to adaptive convergence.

The wrapping behaviour of two species of *Lycosa* (Rovner and Knost 1974) is similar in several respects. The spider stands over the prey and turns, repeatedly attaching silk to the substrate. It also holds the prey with its chelicerae during the first part of wrapping, and then leaves it on the substrate while it continues to turn. Throughout the process the palps are used to contact the prey. Rovner and Knost did not note details of spinneret positions, however, so the possible homology of this behaviour with the behaviour described here is not certain. One difference was that these spiders did not break wrapping lines when lifting the prey after it was wrapped. This may be an adaptation to prevent loss of prey from the elevated wrapping sites (Rovner and Knost 1974) (which was not a problem for our three species).

The psechrid *Feneicia* sp. wraps apparently immobilized prey in a way that may be quite similar to the behaviour reported here for *Tengella radiata*: the spider “binds prey by circling around the insect, attaching silk directly from the spinnerets to the prey surface and/or to the substrate” (Robinson and Lubin 1979, p 140). Wrapping behaviour without use of legs IV may also occur in the diplurid *Ischnothele* (“applying silk to the retreat wall immediately after returning to the retreat”) (Coyle and Ketner 1990). This is not certain, however, as no details were given regarding the sequences of attachments and positions and movements of spinnerets.

The use of body movements in attack wrapping to pull and apply silk to the prey without direct involvement of legs IV has also evolved, probably independently, in several other entelegyne groups, including Oecobiidae (Glatz 1967), Hersiliidae (Dippenaar-Schoeman and Jocqué 1997), and Gnaphosidae (Bristowe 1958). In these groups the spider runs rapidly around and over the prey. Perhaps these convergences are in part due to the fact that little additional dexterity in manipulating lines is needed to run past and over the prey and tangle it in drag lines.

Pull wrapping silk with legs IV. If the wrapping behaviour in the species of Theraphosidae, Tenebrionidae, and Agelenidae is homologous, then the use of legs IV to apply wrapping silk to the prey has evolved convergently in web-building species in at least four and perhaps

five different araneomorph lineages. These include Gradungulidae (Gray 1983) and Austrochilidae (Lopardo et al. 2003) (in both families wrapping is initiated after the prey has been bitten) (in Hypochilidae no wrapping was observed by Shear 1969); Filistatidae (most wrapping was initiated after the prey was bitten but occasionally slightly before); Orbicularia (in some wrapping was initiated before biting, in others after); Pholcidae (wrapping was initiated prior to biting the prey); and Scytodidae (wrapping was initiated before the prey was bitten but after it had been immobilized by sticky silk from the chelicerae). As noted by Robinson (1975), effective wrapping (especially immobilization wrapping initiated while the prey is still struggling) involves complex orientation and coordinated movements of legs IV to grasp, pull, apply, and then release silk lines, so these convergences involve multiple traits.

Use of legs IV to wrap is probably widespread in pholcids (Kirchner and Opderbeck 1990; Huber 1998). Independent derivation of the use of legs IV to wrap in Pholcidae and Scytodidae is supported (if the phylogeny presented by Coddington 2005 is correct, and if use of alternate legs IV does not “regress” to more direct use of the abdomen that does not require the ability to seize and release lines with legs IV) by the fact that spiders in Diguetae and Dyrmusidae each utilize different styles of wrapping that do not involve applying silk to the prey with legs IV. Support also comes from the fact that wrapping was absent in the web-building ochyroceratid *Ochyrocera*, though our small sample size and the well-known variability of attack behaviour (Robinson and Olizarri 1971; Lubin 1980; Japyassú and Caires forthcoming) leaves open the possibility that it may sometimes occur. The diguetid *Digueta albolineata* (O. P.-Cambridge, 1895) does not manipulate wrapping lines directly with its legs IV, and instead pulls silk from its spinnerets by rotating its prey with its anterior legs after the prey is freed from the web (Eberhard 1967). The drymusid *Drymusa dinora* Valerio, 1971 also pulls wrapping silk without using any legs, by dabbing its spinnerets repeatedly against the prey (Valerio 1974). One alternative is that pholcids and scytodids are more closely related than is hypothesized in this phylogeny, and are descended from a common ancestor that used its legs IV to apply wrapping lines to prey.

The relative uniformity of theridiid attack behaviour—early use of sticky silk applied mostly with simultaneous movements of legs IV, later use of non-sticky silk applied mostly with alternate movements of legs IV (see also García and Japyassú 2005 on *Theridion evexum* in Brazil)—is striking in view of the variety of physical contexts in which attack wrapping occurred (from single sticky or non-sticky lines to a dense horizontal sheet of silk between the prey and the spider). Simultaneous application of wrapping silk with both legs IV early in attacks occurred in all of the 12 species of theridiids we observed, and also occurs in two other theridiids, *Ariamnes* (= *Argyrodes*) *attenuatus* O. P.-Cambridge 1881 (Eberhard 1980a) and *Achaearanea digitus* Buckup and Marques (H. Japyassú, personal communication). Another theridiid, *Euryopsis funebris* (Hentz, 1850), also wraps prey (ants) with adhesive-laden silk (Carico 1978), but details regarding alternate versus simultaneous movements of legs IV are not known. On the basis of outgroup comparisons, simultaneous movement of legs IV to apply wrapping lines is apparently derived, and its occurrence in the nesticid and synotaxid in this study may be a synapomorphy linking theridiids with these two families. Robinson and Olizarri (1971) noted that in the early stages of attack wrapping by the araneid *Argiope argentata* (Fabricius, 1775) “both legs IV pick up silk and cast it in nearly synchronous movements”. This description differs from the “simultaneous” wrapping we described above, in which one leg IV seizes silk but then pauses for a moment until the second leg IV has also seized it before applying it simultaneously with both to the prey (Figures 6–8).

Simultaneous movements of legs IV and the use of sticky wrapping lines were often associated during the initial stages of the attacks of theridiids, but they are apparently evolutionarily independent. Simultaneous leg IV wrapping movements occurred in the araneid, *Azilia affinis* (Figure 9), a species which did not produce sticky wrapping lines. This genus is not closely related to theridiids, so this wrapping behaviour seems likely to be convergent. Preliminary molecular data show that *Azilia* is difficult to place among orb weavers (F. Álvarez-Padilla, personal communication). In sum, simultaneous wrapping movements may have evolved once, apparently prior to sticky wrapping lines, in the common ancestor of synotaxids and theridiids and nesticids (see previous paragraph), and independently in *Azilia*, again without sticky wrapping lines (Figure 10).

The association between sticky wrapping lines and the comb of serrated setae on the ventral surface of tarsus IV that is evident in theridiids (Agnarsson 2004) and also in pholcids (Kirchner and Opderbeck 1990; W. G. Eberhard and G. Barrantes, in preparation) also may not extend to other groups. *Synotaxus* sp. has the serrated bristles, although those of *Synotaxus* “share little similarity with the theridiid comb” (Agnarsson 2003, p 722); but we failed in five different observations of one or (probably) two species of *Synotaxus* to confirm the claim (Griswold et al. 1998) that synotaxid wrapping silk is covered with sticky (aggregate gland) material. The reason for this lack of agreement is not clear (species differences? different prey? imprecise observations?). Further work is needed to clear up this mystery.

The proposal in Figure 10 requires the repeated loss of the probable advantages conferred by attacking prey by wrapping them in silk (Robinson et al. 1969; Robinson and Mirick 1971) in linyphiids, tetragnathids, the specialized araneid *Chorizopes* that preys on spiders, and gasteracanthine araneids. Nevertheless, wrapping probably also has costs, such as silk that is expended and not recovered (Weng et al. forthcoming), and also increased prey escapes (see Robinson 1975; Lubin 1980). Immobilization wrapping has also secondarily become strongly reduced in still another group, *Anelosimus studiosus* (Table II). The reasons for the partial loss of immobilization wrapping in this species are not clear; but the consistent use of immobilization wrapping by the congeneric *A. pacificus* and *A. eximius* (L. Avilés, personal communication), as well as by species in other theridiid genera, strongly supports the hypothesis of a secondary reduction in *A. studiosus*.

The loss of immobilization wrapping in linyphiids may be associated with their webs, which partially isolate them from their prey: the spider moves on the underside of a dense horizontal sheet, while the prey is above the sheet. Immobilization wrapping with such a web would be less effective because the sheet forms a barrier to attempts to apply wrapping lines to the prey (Lubin 1980). In addition, the increase in protection afforded by wrapping may also be reduced, because biting attacks would be less risky because of the sheet, which would largely protect the spider from the prey's struggles (Robinson 1975; Lubin 1980). The hypothesis that a dense horizontal sheet with the spider beneath it and the prey above it may favour loss of immobilization wrapping is supported by the behaviour of *Kapogea* sp. and of several species of *Cyrtophora* (Lubin 1980). These species are closely related to araneids such as *Argiope* that build orbs (Griswold et al. 1998) and utilize immobilization wrapping (Robinson and Olizarri 1971), but build dense horizontal sheets rather than in orbs, and they generally attack prey from under the sheet by biting rather than wrapping (Table II; Lubin 1980), although they do wrap some potentially dangerous prey (Lubin 1980; our failure to see wrap attacks in *Kapogea* may be due to our small sample size). Still another detail that fits this idea is that adult females of *Cyrtophora citricola*, which also make a dense horizontal sheet, do perform immobilization wrapping on copulating males, which

occur on the same side of the sheet as the female (Blanke 1972). Effective immobilization wrapping attacks were performed by three theridiids from under dense horizontal sheet webs, *Achaearana tessellata*, *Chrosiothes* sp. nr. *porteri*, and also *Steatoda* (= *Lithyphantes*) *paykulliana* (Walckenaer, 1805) (Kullmann 1964). But in all these species, the wrapping lines were coated with abundant glue, and are thus more likely than are the non-sticky wrapping lines of linyphiids to be able to restrain the prey despite the barrier of the sheet.

The loss of immobilization wrapping in one araneid, the spider predator *Chorizopes* sp., is presumably related to its large chelicerae, apparently strong venom, and its surprise attack tactic (Eberhard 1983). But the loss of immobilization wrapping in the orb-weaving tetragnathids and gasteracanthine araneids (Figure 10) cannot be explained in these ways. One less parsimonious alternative to the scheme in Figure 10 that would reduce the number of evolutionary losses of immobilization wrapping would be to suppose that immobilization wrapping was absent in the common ancestor of Orbiculariae, and was acquired independently in deinopoids (Robinson and Robinson 1971), theridiids and related families, some araneids, and some tetragnathoids. Rotisserie wrapping is present in only one of these groups (araneids), contrary to the claim of Scharff and Coddington (1997) that it occurs in tetragnathids and deinopoids (apparently their conclusions were based on a different definition of rotisserie wrapping). This is in accord with an independent derivation in araneines. Even this hypothesis would require, however, subsequent loss of immobilization wrapping in *A. studiosus*.

Acknowledgements

We thank Ingi Agnarsson, Bernhard Huber, H. W. Levi, Brent Opell, G. Hormiga and Darrell Ubick for kindly identifying specimens, Julin Weng for checking for evidence of glue on nesticid wrapping lines, Glauco Machado for invaluable help arranging field work, Hilton Japyassú for unpublished observations, an anonymous referee for valuable suggestions, and STRI and the Universidad de Costa Rica for financial support.

References

- Agnarsson I. 2003. The phylogenetic placement and circumscription of the genus *Synotaxus* (Araneae: Synotaxidae), a new species from Guyana, and notes on theridiid phylogeny. *Invertebrate Systematics* 17:719–734.
- Agnarsson I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). *Zoological Journal of the Linnean Society* 141:447–626.
- Arnedo MA, Coddington JA, Agnarsson I, Gillespie RG. 2004. From a comb to a tree: phylogenetic relationships of the comb-footed spiders (Araneae, Theridiidae) inferred from nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution* 31:225–245.
- Blanke R. 1972. Untersuchungen zur Ökophysiologie und Ökethologie von *Cyrtophora citricola* Forskål (Araneae, Araneidae) in Andalusien. *Forma et Functio* 5:125–206.
- Bristowe WS. 1958. *The world of spiders*. London: Norton.
- Carico JE. 1978. Predatory behavior in *Euryopsis funebris* (Hentz) (Araneae: Theridiidae) and the evolutionary significance of web reduction. *Symposia of the Zoological Society of London* 42:51–58.
- Coddington JA. 2005. Phylogeny and classification of spiders. In: Ubick D, Paquin P, Cushing PE, Roth V, editors. *Spiders of North America: an identification manual*. American Arachnological Society. www.americanarachnology.org, p 18–24.
- Coyle FA, Ketner ND. 1990. Observations on the prey and prey capture behaviour of the funnelweb mygalomorph spider genus *Ischmothele* (Araneae, Dipluridae). *Bulletin of the British Arachnological Society* 8:97–104.
- Crome W. 1956. Kokonbau und Eiablage einiger Kreuzspinnenarten des Genus *Araneus*. *Deutsche Entomologische Zeitschrift (NF)* 3:28–55.

- Dippenaar-Schoeman AS, Jocqué R. 1997. African spiders: an identification manual. Pretoria: Plant Protection Research Institute. (Plant Protection Research Institute handbook; 9).
- Eberhard WG. 1967. Attack behavior of diguetid spiders and the origin of prey wrapping in spiders. *Psyche* 74:173–181.
- Eberhard WG. 1980a. *Argyrodes attenuatus*: a web that is not asnare. *Psyche* 86:407–413.
- Eberhard WG. 1980b. The natural history and behavior of the bolas spider *Mastophora dizzydeani* sp. n. (Araneidae). *Psyche* 87:143–169.
- Eberhard WG. 1981. The single line web of *Phoroncidia studo* Levi (Araneae: Theridiidae): a prey attractant? *Journal of Arachnology* 9:229–232.
- Eberhard WG. 1982. Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* 36:1067–1095.
- Eberhard WG. 1983. Predatory behaviour of an assassin spider, *Chorizopes* sp. (Araneidae), and the defensive behaviour of its prey. *Journal of the Bombay Natural History Society* 79:522–524.
- Eberhard WG. 1986. Subsocial behavior in the spitting spider *Scytodes intricata* (Araneae, Scytodidae). *Revue Arachnologique* 7:35–40.
- Eberhard WG, Agnarsson I, Levi HW. The webs of Theridiidae: chaos from order. *Biodiversity and Systematics*. Forthcoming.
- Eberhard WG, Barrantes G, Weng J. 2006. Tie them up tight: *Philoponella vicina* spiders mangle and kill their prey by wrapping. *Naturwissenschaften* 93:251–254.
- Fischer ML, Vasconcelos-Neto J. 2005. Parameters affecting fecundity of *Loxosceles intermedia* Mello-Leitão 1934 (Araneae, Sicariidae). *Journal of Arachnology* 33:670–680.
- Foelix R. 1996. *Biology of spiders*. New York: Oxford University Press.
- García C, Japyassú HF. 2005. Plasticity and stereotypy in the predatory sequence of the spider *Theridion evexum* Keyserling, 1884 (Araneae, Theridiidae). *Biota Neotropica* 51A.
- Glatz L. 1967. Zur Biologie und Morphologie von *Oecobius annulipes* Lucas (Araneae, Oecobiidae). *Zeitschrift für Morphologie der Tiere* 61:185–214.
- Gray M. 1983. The male of *Progradungula carraiensis* Forster and Gray (Araneae, Gradungulidae) with observations on the web and prey capture. *Proceedings of the Linnean Society of New South Wales* 107:51–58.
- Griswold CE, Coddington JA, Hormiga G, Scharff N. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneioidea). *Zoological Journal of the Linnean Society* 123:1–99.
- Holm A. 1940. Studien über die Entwicklung und Entwicklungsbiologie der Spinnen. *Zoologische Bijdragen (Uppsala)* 19:1–214.
- Huber BA. 1998. Genital mechanics in some neotropical pholcid spiders (Araneae: Pholcidae), with implications for systematics. *Journal of Zoology (London)* 244:587–599.
- Japyassú HF, Caires RA. Hunting tactics in a cobweb spider (Araneae—Theridiidae) and the evolution of behavioral repertoires. *Journal of Insect Behavior*. Forthcoming.
- Kaston BJ. 1964. The evolution of spider webs. *American Zoologist* 4:191–207.
- Kirchner W, Opderbeck M. 1990. Beuteerweb, Giftwirkung und Nahrungsaufnahme bei der Zitterspinne *Pholcus phalangioides* (Araneae, Pholcidae). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 31/32:15–45.
- Kullmann E. 1961. Der Eierkokonbau von *Cyrtophora citricola* Forskål (Araneae, Araneidae). *Zoologische Jahrbücher Systematik* 89:369–406.
- Kullmann E. 1964. Neue Ergebnisse über den Netzbau und das Sexualverhalten einiger Spinnenarten (*Cresmatoneta mutinensis*, *Drapestica socialis*, *Lithyphantes paykullianus*, *Cyrtophora citricola*). *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 2:41–122.
- Levi HW. 1980. The orb-weaver genus *Mecynogea*, the subfamily Metinae and the genera *Pachygnatha*, *Glenognatha* and *Azilia* of the subfamily Tetragnathinae North of Mexico (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 149:1–74.
- Levi HW. 1997. The American orb weavers of the genera *Mecynogea*, *Manogea*, *Kapogea* and *Cyrtophora* (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 155:215–255.
- Lopardo L, Ramirez RJ, Grismado C, Compagnucci LA. 2003. Web building behavior and the phylogeny of austrochiline spiders. *Journal of Arachnology* 32:42–54.
- Lubin YD. 1980. The predatory behavior of *Cyrtophora* (Araneae, Araneidae). *Journal of Arachnology* 8:159–183.
- Nitzsche ROM. 1988. “Brautgeschenk” und Umspinnen der Beute bei *Pisaura mirabilis*, *Dolomedes fimbriatus*, und *Thaumasia uncata* (Arachnida, Araneida, Pisauridae). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 30:353–393.

- Peters HM. 1931. Die Fanghandlung der Kreuzspinne (*Epeira diademata* L.). Experimentelle Analysen des Verhaltens. Zeitschrift für Vergleichende Physiologie 15:693–748.
- Peters HM. 1933. Weitere Untersuchungen über die Fanghandlung der Kreuzspinne (*Epeira diademata* Cl.). Zeitschrift für Vergleichende Physiologie 19:47–67.
- Robinson MH. 1969. Predatory behavior of *Argiope argentata* (Fabricius). American Zoologist 9:161–173.
- Robinson MH. 1975. The evolution of predatory behaviour in araneid spiders. In: Baerends G, Beer C, Manning A, editors. Function and evolution in behaviour. Oxford: Clarendon Press. p 292–312.
- Robinson MH, Lubin YD. 1979. Specialists and generalists: the ecology and behavior of some web-building spiders from Papua New Guinea I. *Herennia ornatisissima*, *Argiope ocyaloides* and *Arachnura melanura* (Araneae: Araneidae). Pacific Insects 21:133–164.
- Robinson MH. 1971. The predatory behavior of the golden-web spider *Nephila clavipes* (Araneae: Araneidae). Psyche 78:123–139.
- Robinson MH, Mirick H, Turner O. 1969. The predatory behavior of some araneid spiders and the origin of immobilization wrapping. Psyche 76:487–501.
- Robinson MH, Olizarri J. 1971. Units of behavior and complex sequences in the predatory behavior of *Argiope argentata* (Fabricius) (Araneae: Araneidae). Smithsonian Contributions to Zoology 65:1–36.
- Robinson MH, Robinson B. 1971. The predatory behavior of the ogre-faced spider *Dinopis longipes* F. Cambridge. American Midland Naturalist 85:85–96.
- Robinson MH, Robinson B. 1973. Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. Smithsonian Contributions to Zoology 149:1–76.
- Robinson MH, Robinson B. 1974. The biology of some *Argiope* species from New Guinea: predatory behavior and stabilimentum construction (Araneae: Araneidae). Zoological Journal of the Linnean Society 54:145–159.
- Robinson MH, Robinson B, Graney W. 1971. The predatory behavior of the nocturnal orb web spider *Eriophora fuliginea* (C. L. Koch) (Araneae: Araneidae). Revista Peruana de Entomologia 14:304–315.
- Rovner JS, Knost SJ. 1974. Post-immobilization wrapping of prey by lycosid spiders of the herbaceous stratum. Psyche 81:398–414.
- Scharff N, Coddington JA. 1997. A phylogenetic analysis of the orb-weaving spider family Araneidae (Arachnida, Araneae). Zoological Journal of the Linnean Society 120:355–434.
- Shear WA. 1969. Observations on the predatory behavior of the spider *Hypochilus gertschi* Hoffman (Hypochilidae). Psyche 76:407–417.
- Shear WA, Palmer JM, Coddington JA, Bonamo PM. 1989. Devonian spinneret: early evidence of spiders and silk use. Science 246:479–481.
- Ubick D. 2005. Filistatidae. In: Ubick D, Paquin P, Cushing PE, Roth V, editors. Spiders of North America: an identification manual. American Arachnological Society. www.americanarachnology.org, p 104–105.
- Valerio CE. 1974. Prey capture by *Drymusa dinora* (Araneae, Scytodidae). Psyche 81:284–287.
- Valerio CE. 1981. Spitting spiders (Araneae, Scytodidae, *Scytodes*) from Central America. Bulletin of the American Museum of Natural History 170:80–89.
- Weng J, Barrantes G, Eberhard WG. Feeding by *Philoponella vicina* (Araneae, Uloboridae) and how uloborids lost their poison glands. Canadian Journal of Zoology. Forthcoming.
- Wolff RJ. 1977. The cribellate genus *Tengella* (Araneae: Tengellidae?). Journal of Arachnology 5:139–144.