SHORT COMMUNICATION

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Tie them up tight: wrapping by *Philoponella vicina* spiders breaks, compresses and sometimes kills their prey

Abstract We show that uloborid spiders, which lack the poison glands typical of nearly all other spiders, employ thousands of wrapping movements with their hind legs and up to hundreds of meters of silk line to make a shroud that applies substantial compressive force to their prey. Shrouds sometimes break the prey's legs, buckle its compound eyes inward, or kill it outright. The compressive force apparently results from the summation of small tensions on sticky lines as they are applied to the prey package. Behavioral details indicate that wrapping is designed to compact prey; in turn, compaction probably functions to facilitate these spiders' unusual method of feeding. This is the first demonstration that prey wrapping by spiders compacts and physically damages their prey, rather than simply restraining them.

Introduction

Spiders are well-known for the venom with which they subdue their prey, but the members of the web-building family, Uloboridae (approximately 300 species, Coddington and Levi 1991), have secondarily lost their venom glands (Opell 1979). Predatory attacks by these spiders are exceptional in that the prey is wrapped in apparently excessive amounts of silk. Previous observations of *Zosis geniculatus* (Lubin 1986) and *Hyptiotes cavatus* (Opell 1988) documented up to 74 min of wrapping that applied up to 80 m of silk to a single prey. Wrapping by *Z. geniculatus* averaged 726 s for small flies (whose wet weight was about 14% of that of the spider), and 2,838 s for large flies (about 76% of the spider's weight) (Lubin 1986). In contrast, araneid orb weavers spend about two orders of magnitude less time wrapping: *Argiope argentata* spent a mean of 26± 42 s wrapping relatively large prey (389±115 mg crickets that were approximately 75% of the spider's typical 500-mg weight; Robinson and Olazarri 1971); *Allocyclosa bifurca* averaged 9.7±3.0 s to wrap 4.6±1.8 mg muscoid flies that averaged about 15% of the spider's weight. The extraordinary investments of uloborids in wrapping are especially striking because much of the wrapping silk is subsequently discarded with the prey remains after feeding (Lubin 1986, Weng et al. unpublished data).

The aim of this paper is to clarify the functional significance of these investments of time, energy, and materials in the uloborid *Philoponella vicina*, a small species (body length about 6 mm, weight 9–14 mg) that builds more or less horizontal orb webs at sheltered sites in tropical forests (Fincke 1981, Eberhard et al. 1993). They are generalist predators; 46 prey being fed on in the field belonged to nine orders, ranging from small compact beetles to long-legged nematocerous flies.

Results and discussion

We observed attacks by mature female *P. vicina* on tipulid, muscoid, and *Drosophila* sp. flies, ants, braconid wasps, moths, leafhoppers, and beetles, using both digital video recordings (30 fps) and direct observations under a dissecting microscope (up to 40×). Wrapping lines were occasionally visible in video recordings, confirming positions of lines deduced from leg and spinneret positions. Prey outlines were experimentally extended by inserting an 11-mm segment of straight human head hair through the thorax of live *Drosophila* sp. flies (Fig. 3c). Silk to be

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viewed in the scanning electron microscope (SEM) was air-dried before being sputter-coated with gold. Means are reported ±1 SD.

Attack and feeding behavior of *P. vicina* did not differ from the relatively stereotyped behavior of other uloborids (Lubin 1986, Opell 1988). Prey was generally wrapped for several minutes at the capture site without being bitten and then carried to a resting site and wrapped further. Attacks on large prey involved up to >28,000 wrapping movements of the hind legs that applied a swath of silk >140 m long that contained at least 10–20 separate lines (Weng et al. unpublished data). Following the second bout of wrapping, the spider wetted the entire surface of the prey package, rotating it with her palps while regurgitating clear digestive fluid onto it. She then fed by cyclically regurgitating and then sucking up fluid from the outer surface of the package. In most cases she never broke open the silk shroud; when finished, she sucked the package dry and dropped it.

The spider's wrapping movements were similar in all attacks (Fig. 1). She rapidly shuttled her abdomen from side to side, and pulled multiple silk lines from her widespread spinnerets with ventral thrusts of her hind legs (IV) that applied the silk to the prey. Experimental extension of the prey's outline led to sharp increases in wrapping movements. When five spiders were each given a *Drosophila* sp. prey with a hair and without a hair (on different days, order of presentation alternated), the mean numbers of wrapping movements more than tripled when the fly had a hair (7,113±1,325 vs 2,264±542; $t=-7.71$ with paired t test, $p=0.0014$; the weight of the hair was approximately 0.088 mg, or <5% of the weight of the fly; the weight of the fly, in turn, was about 10% of that of the spider).

Two patterns in wrapping behavior made wrapping particularly effective at compacting prey. Early in attacks on especially bulky prey (five long-legged tipulid flies, 12 *Drosophila* sp. with a hair), one leg IV applied silk at one edge of the prey package while the other applied it to the central portion (Fig. 2a). The tension exerted by the lines (see below) thus gradually pulled the edge of the package toward the center. Later, when the prey bundle was compact enough for the spider to span it, each leg IV applied silk to a lateral edge of the package, pulling both edges toward the center (Fig. 2c–e). In addition, the spider tended to hold elongate prey so its longest axis was approximately parallel to the spider's ventral plane and perpendicular to her longitudinal axis during wrapping (Figs. 1 and 2), a position in which tensions exerted by wrapping lines shortened the prey package. When the position of a *Drosophila* sp. prey with a hair was noted every 15 s during the early stages of wrapping (before the hair had been bent into a "U" of <110°), the long axis of the hair was always more nearly parallel than perpendicular to the spider's ventral plane ($N=101$ observations of seven attacks by as many spiders; $p<0.0001$ analyzed by cases, $p=0.008$ analyzed by different individual spiders; binomial tests). It was also within 15° of the spider's transverse axis (as in Fig. 1) in 83 of 101 cases. This alignment with her transverse axis was significantly more common than the other equally possible alignments (16–90°) for each of the seven spiders (p ranged from 0.004 to<0.0001 for different spiders; $p=0.008$ analyzed by more nearly parallel or perpendicular for different individual spiders; binomial test).

There was no sign of free liquid on wrapping lines (Fig. 3g), but two types of evidence indicated that at least some lines were sticky when they were applied to the prey. The thinner of the two sizes of lines adhered to each other (Fig. 3g); some lines conformed to small details in the relief on the prey's surface (Fig. 3f). Struggling movements of *Drosophila* sp. flies in only partially complete shrouds (wrapping was interrupted by frightening the spider) showed that some legs, which touched the inner surface of the shroud but were not tangled with any lines, nevertheless did not come free when the fly lifted them,
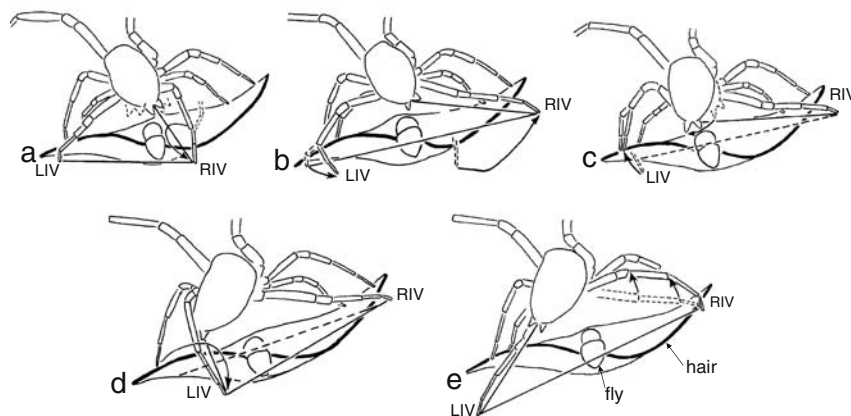

Fig. 1 Stylized representation of 0.33 s of an early stage of wrapping of a *Drosophila* sp. fly transversed by a hair, when the hair had been bent only slightly (drawn from video images). The right hind tarsus (RIV) pulls out line in **a**, and applies it to the right edge of the prey bundle in **b** and **c**, while the abdomen swings to the left. The left hind tarsus (LIV) grasps and pulls wrapping line in **d**, then swings toward the prey in **e** as RIV releases its hold on prey and prepares to grasp the line again near the spinnerets and the abdomen swings to the right. *Dotted lines* indicate lines already applied to the prey. Simplifications in the drawings include the following: distal segments of legs I are omitted; only a single wrapping line is drawn as emerging from the abdomen tip (instead of the 10–20 lines from each posterior median spinneret); wrapping lines are drawn as being held by a single point on tarsus IV (instead of by the wrapping comb on the ventral surface of the tarsus and metatarsus)
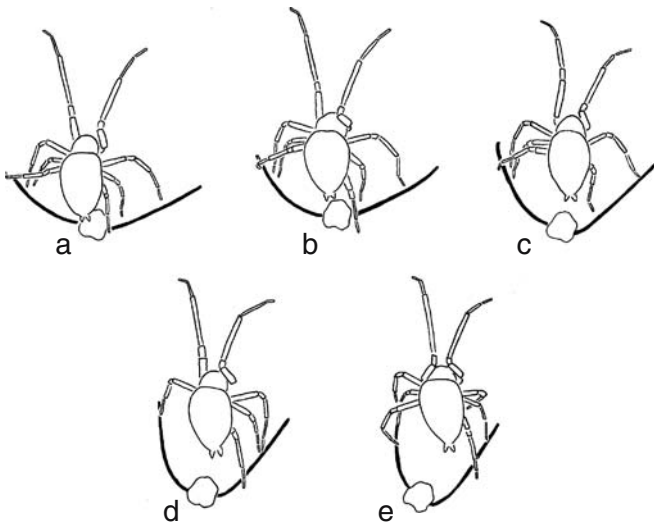
Fig. 2 Stylized depiction of gradual bending of a human hair drawn from video images. Time elapsed from **a** to **e** was about 8 mins 35 s

Substantial tensions were produced by wrapping. For instance, the elongate outlines of tipulid flies (Fig. 3a) were gradually reduced to compact packages (Fig. 3b). Wrapping sometimes seriously damaged prey. In three *Drosophila* sp., at least one compound eye had buckled inward by the time wrapping was finished. The femora and tibiae of long-legged tipulid flies in discarded prey packages were bent and broken (arrows in Fig. 3e). Wrapping sometimes killed prey. Five muscoid flies (about 14 mg) were removed from the spider at the end of wrapping (as the spider shifted the prey to its palps and chelicerae just before wetting it and beginning to feed). When the shrouds were broken open, three flies were apparently dead, and another struggled feebly and did not recover. Presumably death was from asphyxiation, caused either by cutting off internal tracheal connections due to severe folding of the body or by restricting body movements needed to flush air through its tracheae (Chapman 1998).

The force produced by wrapping was many times the spider's own weight. The force needed to bend or break the femur of one leg of the tipulid species in Fig. 3 was measured by gluing the femur near its base to a wooden dowel, and a small copper hook (0.5 mg) to its tip; then other hooks (6.8 mg each) were hung from this hook until the femur bent sharply or broke. It took 81 mg applied
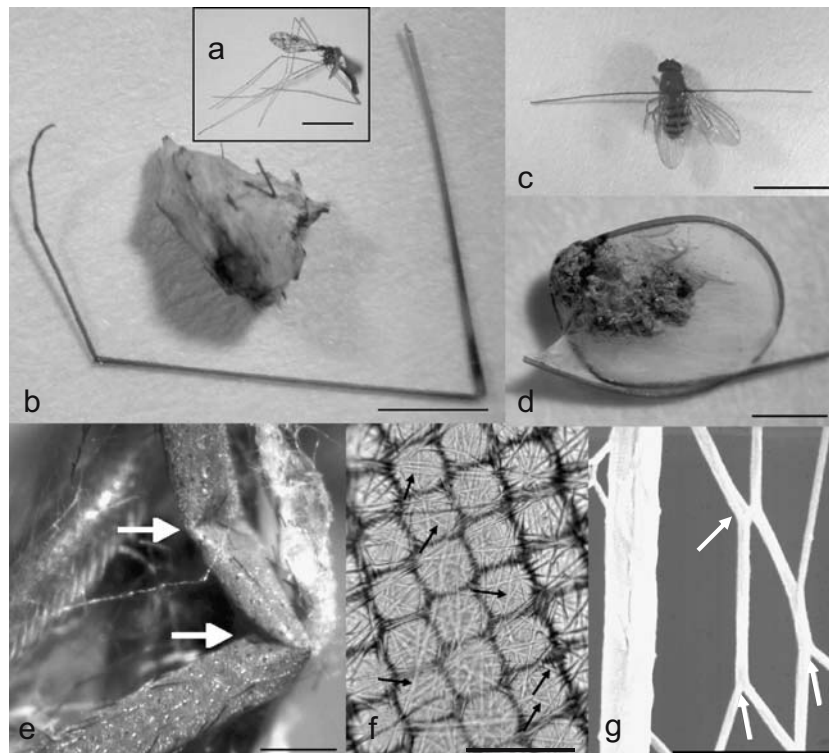
and pulled on the shroud. The mechanism of adhesion is not clear. Van der Waals forces acting over substantial areas of contact might explain adhesion between lines such as those in Fig. 3g, but are less likely to explain adhesion to the bristly surface of a fly leg.

Fig. 3 **a** A tipulid fly from which one leg was removed before it was wrapped and fed on by a *P. vicina* spider. **b** Leg and wrapped package containing the rest of fly in **a**. **c** and **d**. A *Drosophila* sp. fly traversed by an 11-mm human hair **c** before and **d** after being wrapped and fed on by a spider. **e**. Bent and crumpled femur (*arrows*) of a tipulid fly leg in a prey package that was opened after the spider fed. **f**. Shroud of silk bearing the imprint of the compound eye of a muscoid fly; it was peeled away from the prey before the spider had regurgitated and begun to feed. **g** Perhaps the imprint was due to the fine adhesive lines, as the *thicker lines* (*arrows*) did not follow the contours of the eye. SEM image of wrapping silk showing large and small diameter lines, sites of adhesion between smaller lines (*arrows*), and lack of free liquid. Scale lines: **a** 2.23 mm, **b** 7.18 mm, **c** 3 mm, **d** 0.85 mm, **e** 1.08 mm, **f** 0.032 mm, and **g** 0.002

perpendicular to the longitudinal axis to break a horizontal, 4.95-mm long section of one femur. This underestimates the force applied by wrapping because leg segments were sometimes broken by forces applied in directions more nearly parallel to their longitudinal axes (e.g., Fig. 3e). In a more realistic test, 367 mg were applied at about a 10° angle to a 5.30-mm section of another femur of the same species before it buckled. Even this is an underestimate of the maximum forces applied because the tibia and femur of a leg were often folded back on each other during wrapping, and multiple legs were often oriented in similar directions. Such multiple segments would have reinforced each other against the compressive forces applied by the shroud, but they nevertheless bent or broke.

How were these large forces produced? The spider's legs IV, whose movements resulted in the gradual compression during wrapping (Figs. 2 and 3), are not obviously modified for strength (Figs. 1 and 2). However, their wrapping movements probably often apply lines under tension to the prey package. Each time the spider grasped the swath near her spinnerets and then increased the distance between the two tarsi IV as she thrust this tarsus IV toward the prey (Fig. 1b,c), the wrapping lines must have been tense when they were applied to the prey package [we know of no studies of the physical properties of wrapping silk, but suppose that, as with all other spider silk (Foelix 1996), wrapping lines are extensible]. Because the wrapping lines are sticky, the tension each new swath of lines exerted on the shroud would be maintained when the spider's tarsus released its hold (Fig. 1d, left IV). Each application of extended sticky wrapping lines to the shroud would result in an increase in the compressive forces it exerted. The thousands of small increments from individual wrapping movements presumably sum up to the large observed compressive forces.

Another possibility is that some sort of chemical change in the lines causes them to contract after they are applied to the prey. We saw no additional bending of two hairs, however, when they were removed from the spider after being partially wrapped and bent to a "U" shape.

The fact that wrapping compresses prey raises the question of the function of compression. Holes in the prey cuticle produced when legs break or eyes collapse could increase the access of the spider's digestive juices to the prey's interior, but we do not believe that this is the function of compressive wrapping. Spiders killed and fed successfully on very hard prey such as beetles and ants, whose legs and other body parts were not broken during wrapping and which were still alive when the wrapping ended, and the spider wetted the prey package. The spider's regurgitated digestive juices apparently digest prey membranes (Eberhard et al. 2006), allowing access of digestive fluid to the prey's interior. Compressive wrapping by uloborids is probably related instead to their unique method of extraoral digestion: they wet the entire outer surface of the prey with digestive juices, and keep it wet for the several hours during which they feed (Lubin 1986; Opell 1988; Eberhard et al. 2006). Other spiders regurgitate digestive juice only onto the portion near the spider's mouth (Bartels 1930; Zimmermann 1934; Kaestner 1968; Collatz 1987; Eberhard et al. 2006). We propose that the function of the apparently excessive wrapping by uloborids is to reduce the surface area that the spider must wet to feed.

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