

Trolling for water striders: active searching for prey and the evolution of reduced webs in the spider *Wendilgarda* sp. (Araneae, Theridiosomatidae)

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Wendilgarda sp. builds unusually simple webs attached to the surface of water. The simplest design consists of a single vertical line with sticky material near the bottom that is attached at the top to a single horizontal line and at the bottom to the water surface. The spider usually sits immobile waiting for prey as the sticky line skates erratically across the surface of the water, but some spiders actively dragged their webs back and forth across the water. The web's simplicity is apparently derived with respect to the webs of other *Wendilgarda* species, as spiders sometimes made more complex webs similar to typical *Wendilgarda* webs. The simplicity of *W.* sp. webs may be causally related to two other unusual traits: extreme variability in web design and construction behaviour and web manipulation behaviour; and construction of prey capture webs with sticky lines by mature males, confirmed here for the first time in a confirmed member of an orb-weaving family. Some behavioural innovations in *Wendilgarda*, such as the attachment of a short segment of non-sticky silk to the water surface just prior to laying each segment of sticky line, may represent blocks of behaviour that have been shifted temporally in the web construction sequence.

KEYWORDS: Spiders, webs, construction behaviour, *Wendilgarda*, behavioural evolution.

Introduction

Most spiders in the genus *Wendilgarda* construct prey capture webs near the surfaces of streams (Coddington and Valerio, 1980; Coddington, 1986; Eberhard, 1989a; Shinkai and Shinkai, 1997). The prey capture portions of a typical web consist of about 20 sticky vertical lines that are 1–4 cm long and attached at their upper ends to a few more or less horizontal, non-sticky suspension lines, and at their lower ends to the surface of a stream (Coddington and Valerio, 1980; Eberhard, 1989a; Shinkai and Shinkai, 1997). Webs are built near stream edges or in the lee of protruding snags, and the suspension lines are attached to objects such as rocks and twigs near the water surface. Construction of other aerial webs attached to the

surface of water also occurs in the closely related theridiosomatid *Epilineutes globosus* (O. Pickard-Cambridge) (Xavier, 1995), and, apparently convergently, in the theridiid *Theridion bergi* Levi (Xavier *et al.*, 1995) and the anapid *Conoculus lyugadinus* Komatsu (Shinkai and Shinkai, 1988).

This paper describes the prey capture web and web construction, and web manipulation behaviour of *W.* sp., which builds reduced versions of typical *Wendilgarda* webs. Web reduction has occurred repeatedly in different groups of spiders (e.g. Kaston, 1964; Carico, 1978), generally associated with increased ability to attract prey (Eberhard, 1980, 1982; Stowe, 1978, 1986; Shinkai, 1988a), an ability to hunt at sites of high prey concentrations (Stowe, 1978; Carico, 1978; Eberhard, 1991), and active manipulation of the web to increase its ability to capture prey (e.g. Kaston, 1964) (some other reductions are of uncertain significance—see Eberhard, 1989a; A. Shinkai, 1988b, 1998; E. Shinkai, 1984 on *Cyrtarachne*). I will argue that web reduction in *W.* sp. was not associated with any of these advantages, but instead with the otherwise unique mobility of the web itself skating over the surface of the water to capture water striders.

Also described are prey capture, behaviour patterns used by the spider to move across the surface of the water, and microscopic details of web structure.

Materials and methods

Observations of *W.* sp. were made on Barro Colorado Island (BCI), at the edge of Gatun Lake, Panama during July to December 1996. Most observations were made along the shore of the lake, but a few spiders were also found with prey capture webs near the mouths of small creeks. Web structure was observed by gently dusting lines with small amounts of cornstarch. Sticky portions of lines were distinguished from others by their coating of small balls that made them appear thicker. Spiders were also observed under a dissecting microscope as they dropped onto the surface of the water in a petri dish.

Attachments of sticky vertical lines to the water surface were collected on microscope slides by bringing the slide up gently under the attachment. Coverslips were fastened to some slides to lift the upper portion of the vertical line and keep the droplets of adhesive free of the slide and permit measurement of their diameters.

An effort was made, both when accumulating observations of web types and of variations in web-building behaviour, to avoid repeating observations of the same individuals by making observations at different sites. A second smaller species of *Wendilgarda* that usually occurred along creek margins on BCI also occurred in low numbers along the margin of the lake. It was difficult to distinguish this species in the field from immatures of *W.* sp. Thus observations involving only field identifications include only those of the unmistakably larger mature males and females of *W.* sp. Large ocean-going ships traversing Gatun Lake passed about 1 km away, and sometimes caused waves and surges that destroyed webs. Observations of web construction by *W. clara* were made during February 1997 at the field station La Selva, Heredia Province, Costa Rica.

Due to the current lack of taxonomists able to devote time to identifications, spiders were identified using published information (Coddington, 1986). Vouchers have been deposited in the US National Museum (Washington, DC) and the Museum of Comparative Zoology (Cambridge, MA). The lack of species identifications made it necessary to presume that the species of *Wendilgarda* studied in Japan by Shinkai and Shinkai (1997) was different from any of the other *Wendilgarda*

species that have been studied (all in Central America), and to refer to the three unidentified species of *Wendilgarda* that have been observed as follows: 'Japanese *W. sp.*' (the species studied by Shinkai and Shinkai, 1997); 'BCI creek *W. sp.*' (small species from creeks on BCI—object of brief observations in the present study) (different from *W. clara* Keyserling which was observed in Costa Rica); and '*W. sp.*' (larger species from the edge of Gatun Lake—the main subject of the present study).

Results

Construction of simple webs

Spiders without prey capture webs rested on more or less horizontal non-sticky lines attached to branches of bushes and trees overhanging the lake up to 10 m from the shore and up to about 4 m above the surface of the water. Web construction, which was observed > 50 times, occurred below overhanging vegetation at various times during the day. A spider sometimes began prey capture web construction by laying or replacing one or more non-sticky lines. The fact that spiders under the microscope nearly always broke the lines where they walked at the same time that they reeled up the line in front of them and released new dragline behind (e.g. figure 1A) suggests that these movements in the field also involved breaking and replacing pre-existing lines, although this detail was seldom confirmed directly.

In many cases the spider passed immediately to the second stage of construction, especially when it was replacing a recently damaged web. Moving along the more or less horizontal 'suspension' line on which it was resting, it reeled up the line ahead of it and at the same time released new dragline behind at a more rapid rate (figure 1A). The more rapid release caused the spider's body to sweep through an arc as it descended (figure 1B). It then turned 180° and attached its dragline, and moved back in the direction from which it had come, again sweeping through an arc as it descended. After descending through up to three or four of these arcs, the spider attached its dragline to the now deeply sagging suspension line and descended vertically to the surface of the water (figure 1C).

Usually the spider attached the dragline to the water surface, then climbed back up about 2–4 cm, turned there, and descended again to the water where it again attached a line to or near the water surface. It then immediately ascended the dragline once again, this time producing a vertical or nearly vertical sticky line (figure 2). It paused briefly about 2 cm up the dragline to pull out additional sticky line from its spinnerets with alternate movements of its legs IV, then attached this line to the vertical non-sticky line, and climbed farther up to the suspension line. At least sometimes the spider reeled in and replaced the vertical line above as it went (figure 2C). Often the junction with the suspension line above moved upward, indicating that this new line was longer than the line it replaced, and that the tension on the vertical line was reduced. The lower end of the vertical line was sometimes displaced laterally as it skated on the surface of the water (see below). Finally, the spider turned to face downward, holding the vertical line it had just laid with one leg I.

In most cases it was not possible to observe whether or not the spider broke and replaced lines as it moved, except to note that the sticky line laid on the second ascent (c–d in figure 2C) clearly sagged away from the intact non-sticky line the spider was ascending, and thus did not replace it. In one case, however, I was able to see that the line laid on the second descent (b–c in figure 2B) was added to and did not replace the line (or lines) laid on the first descent and ascent (a–b and b–a

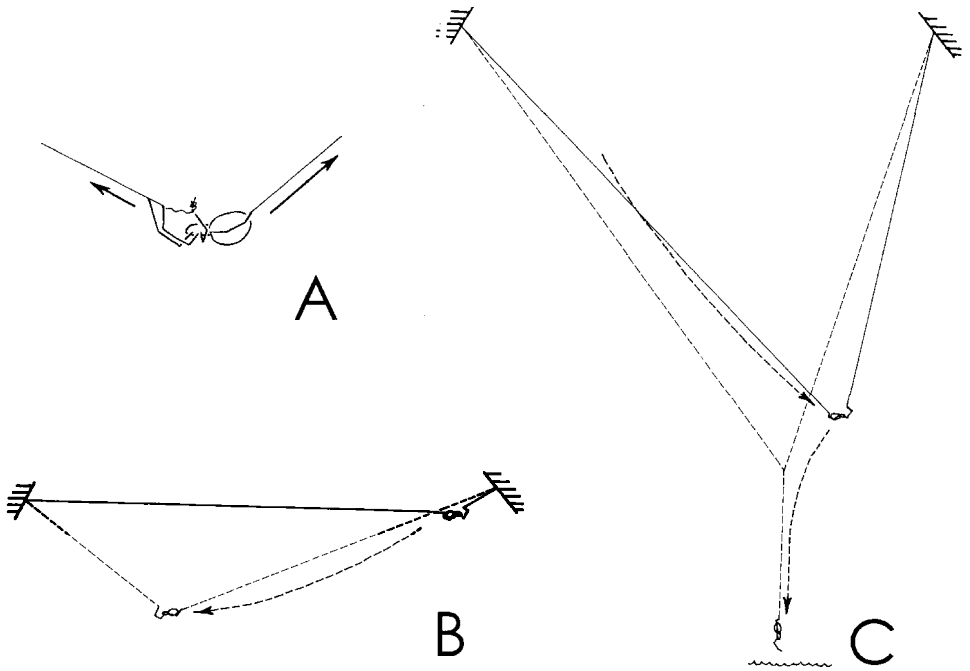


FIG. 1. Events during the descent to attach a line to the water surface (schematic and not to scale). The spider produced new silk more rapidly than it reeled up the line where it walked (lengths of arrows in A), causing it to descend in arcs (arrows in B and C) (dotted lines indicate later positions of web lines). The final portion of the descent was straight downward at the end of a dragline (C).

in figure 2A). Details of the morphology of the attachment to the water and the vertical line with the balls of sticky material (below) indicate that the spider almost certainly did not make a second attachment to the water surface on the second descent (i.e. that c was just above a as in figure 2B).

The point of attachment of each sticky line to the water was often marked by an upward-projecting dimple in the water's surface (e.g. figures 2, 3), indicating that the line was under tension. The heights of different dimples increased and decreased, indicating that tensions were not constant. Sometimes the vertical line of a web with a single vertical line was quite slack, so that when the wind blew or there was a current in the water below, the lower end of the line was displaced laterally up to 25 cm from directly below the upper end of the line, and (with wind) the line was bowed. Slack lines of this sort were not simply the result of increases in water level, as they occurred in freshly made webs built when no water level changes had occurred. The site of the attachment to the water skated erratically and sometimes relatively rapidly over the surface, moving in an area below the upper end of the line that in some cases was as much as an estimated 700 cm². Estimated rates of movement of attachment points across the water surface reached up to 1–5 cm/s.

Webs were sometimes destroyed when leaves, twigs or other objects floated past, when wind caused web supports to move or produced waves in the water, or when the water level dropped briefly when a ship passed by. When an attachment popped free from the water surface, the spider quickly reeled in the dangling line and appeared to ingest it. When the line snagged on a small piece of detritus and the

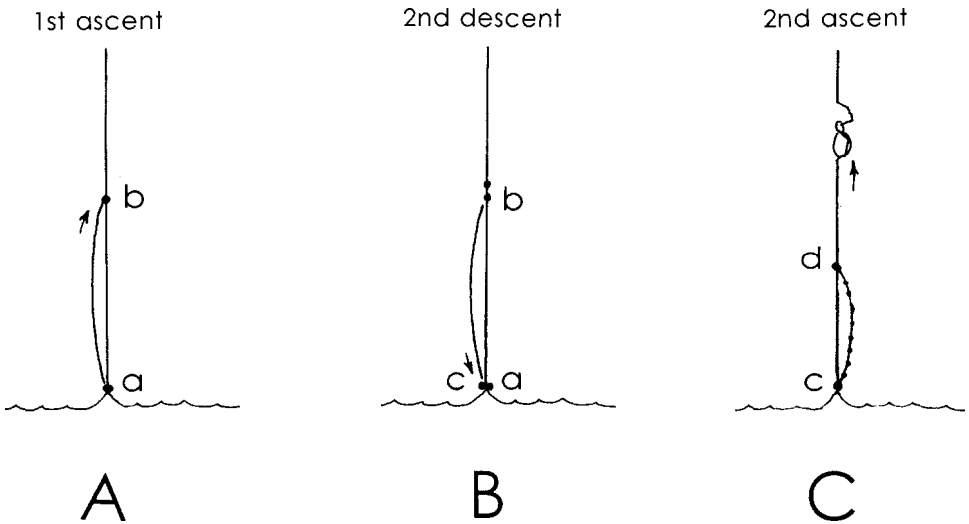


FIG. 2. Probable sequence of attachments by *W. sp.* near the water surface (schematic and not to scale). It was not clear from behavioural observations whether line a-b was doubled (as in drawing A) or broken and replaced (as it probably is in *W. clara*); nor was it certain whether point c was on the surface of the water or, more likely, just above it (see figure 7). It was confirmed repeatedly, however, that the sticky line c-d (with balls in drawing C) was added to the non-sticky line rather than replacing it, as the sticky line was seen sagging briefly away from the straight vertical line. In two cases favourable lighting angles and background allowed confirmation that line b-c was added to rather than replaced the line or lines laid just previously (a-b).

detritus was pulled up free of the water, the spider reeled up the line, removed the attachment to the detritus and dropped the detritus to the water below. Sometimes spiders pulled undamaged webs from the water and ingested them. Spiders often replaced damaged webs quickly, as soon as one minute later. One individual, for example, made six webs in the space of 51 min. The average dimensions of webs of mature females are given in table 1.

Construction of more complex webs

In some cases a single vertical line with a short section of sticky silk at the lower end was all the prey capture web that the spider made. In other cases the spider

Table 1. Dimensions of webs of mature female *W. sp.* and mature and penultimate female *W. clara*.

	<i>W. sp.</i>			<i>W. clara</i>		
	Mean	Range	<i>N</i>	Mean	Range	<i>N</i>
Number of suspension lines	1.1+0.4	(1-3)	76	3.3+0.5	(3-4)	11
Height of spider over water (cm)						
Single vertical line webs	25.4+19.6	(8-80)	26			
Multiple vertical line webs	12.7+8.2	(5-31)	15	3.6+1.2	(2-9)	8
Length of suspension line (cm)						
Single vertical line webs	86.4+61.8	(12-210)	11			
Multiple vertical line webs	67.0+30.3	(49-102)	3	8.8+4.6	(5-22)	19

added further sticky lines. In one common type of modification (figure 3A), the spider again descended the vertical line it had just made, apparently attaching a line to it a short distance above the sticky portion, and then repeating the double descent–double ascent behaviour described in figure 2. Sometimes a third short line of this sort was added before the spider became immobile at the top of the vertical line.

A second type of additional sticky line was begun with a second attachment to the suspension line, either at the point where the first line was attached or up to 1–3 cm away. The spider descended to the water, performed the double descent–double ascent behaviour described in figure 2, and then climbed back to the suspension line, which it broke and reeled in while moving toward the first vertical line. The second vertical line was then attached to the suspension line at or near the top of the first vertical line (figure 3B). The upper portions of such vertical lines almost always subsequently became entangled and merged to assume the form illustrated in figure 3A. Sometimes a third vertical line was laid and then combined with the first two. In webs with multiple attachments to the water (below) the dimples of different attachment points stayed apart instead of collapsing together when multiple sticky lines that were brought together at their attachments above to the suspension line and merged along most of their length. This displacement of the attachments may be due to the array of fine lines comprising the attachment discs to the water (below). A third type of construction was similar to that just described except that the tops of the two vertical lines were not brought together, and then further vertical lines (up to 11) were attached to the same suspension line, thus resembling more

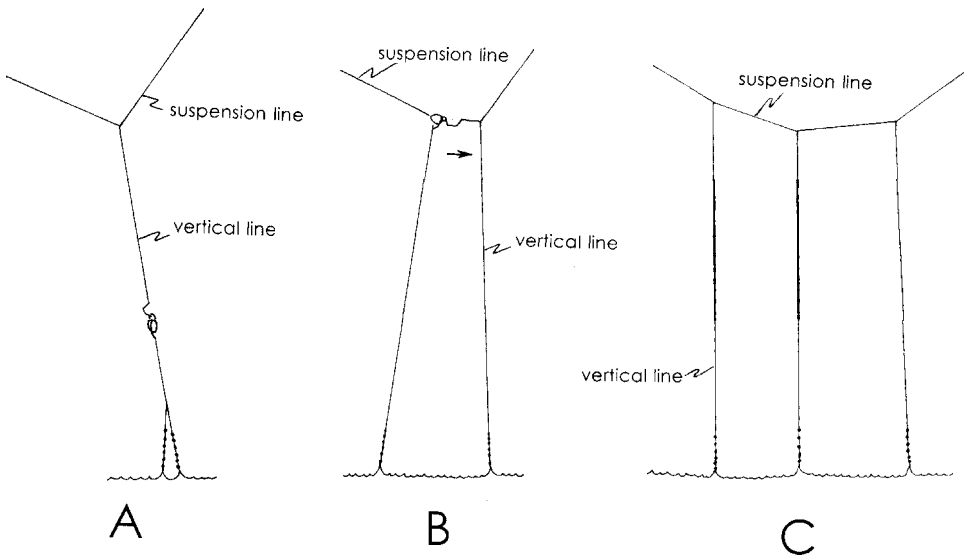


FIG. 3. Construction of three types of webs (schematic and not to scale; black balls represent sticky material). (A) The spider climbs to the suspension line after laying an additional short line to the water that was attached to the first vertical line a few centimetres above the water's surface. (B) Spider moves a second vertical line (arrow) so its upper end will be close to or attached to that of the first vertical line. Usually the upper portions of the two vertical lines then merged, resulting in a configuration like that in (A). (C) Three vertical lines were attached to the suspension line and not subsequently moved.

typical *Wendilgarda* webs (figure 3C). A few webs had multiple suspension lines (up to three) (table 1).

I observed the complete construction process of 14 webs with multiple vertical lines. In all cases, each vertical line was laid with a double descent to the water's surface as in figure 2. Successive vertical lines were added to one end of the array of lines in 86 of 90 cases. In five cases which were observed especially closely, the spider made a particular series of movements when it reached the upper end of a new vertical line after the double descent to the water. It first faced along the suspension line toward the other vertical line or lines that were already in place, and in some cases reeled in a short portion of the suspension line, thus decreasing the distance between the top of the new vertical line and the previous vertical lines (figure 4A). Then it turned 180°, attached its dragline to the suspension line, and either walked along it away from the previous vertical lines or paid out a short length of dragline, causing the previous vertical lines to move slightly away from the spider (figure 4). Then the spider attached its dragline again to the suspension line and descended to the water to begin construction of the next vertical line. Often it dropped to the water at nearly the same site as when it laid the previous vertical line. In one carefully observed case the spider moved laterally only 4 cm during the construction of the second through sixth vertical lines, while the first vertical line it had made moved 11 cm in the opposite direction.

There was substantial variation in the details of construction behaviour of webs

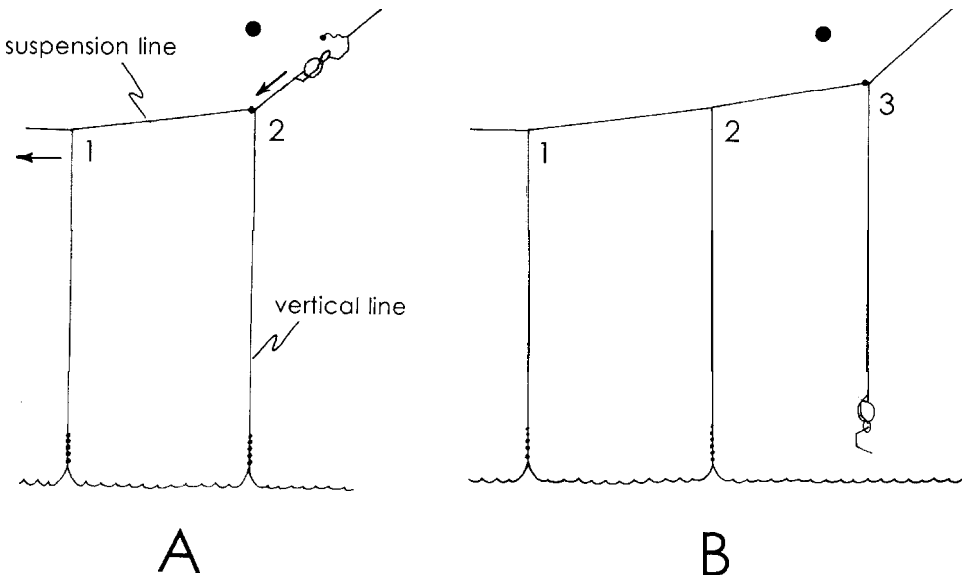


FIG. 4. Production of successive vertical sticky lines (schematic and not to scale). After moving slightly toward previous vertical lines and attaching the vertical line it had just laid (2) to the suspension line, the spider turned 180°, attached its dragline to the broken end of the suspension line (small dot at the top of vertical line 2), and released silk, causing the two vertical lines to move away from it (arrow in (A); large dot gives a fixed point of reference). Then it joined the broken ends of the suspension line (small dot at top of vertical line 3 in (B)), and descended to the water to make the next vertical line. Exact sites of broken ends of lines are estimated, as they were not observed directly.

with multiple vertical lines. In some cases the spider cut the connection of the first vertical line to the suspension line just after it was finished and carried the line 5–10 cm along the suspension line, then attached it again and proceeded to lay a series of additional vertical lines moving back in the direction from which it had come. When the spider had two suspension lines, successive vertical lines were usually but not always laid under the same suspension line. In one case a spider laid a series of vertical lines attached to one suspension line, another series attached to another, and then laid an additional vertical line attached to the first. In another web the spider laid three vertical lines attached to one suspension line, then readjusted the connections between this suspension line and other non-sticky lines (including a second suspension line), and then laid a series of vertical lines attached to the second suspension line.

Of 76 webs of mature females, 61.8% had only a single vertical line; 53% of these had a single sticky line attached to the water, 36% had two attachments and 11% had three. Of the 29 webs with multiple vertical lines, 72.4% had only a single suspension line, 24% had two suspension lines and 3% had three. When the connections with the water were experimentally destroyed in 31 different webs without breaking any suspension lines, the spider tended to make a similar type of replacement web (single versus multiple vertical lines, $\chi^2 = 20$, $df = 1$, $P < 0.001$). In some cases, however, a spider made a quite different web. Of 15 spiders (excluding mature males) that were found with webs that had only a single vertical line, 13% built replacement webs with more than one vertical line (e.g. figure 3C); of 16 found with webs with multiple vertical lines, 25% built replacement webs with only a single vertical line (e.g. figure 3A). Two spiders replaced a single vertical line web with multiple vertical line webs with two suspension lines; and one spider replaced a two suspension line and 14 vertical line web with a single vertical line.

There was no clear difference in the web types of early instar nymphs and mature females. The webs of first instar spiders were seldom or perhaps never observed. Of 15 webs of immature spiders, 40% had only a single line, and 78% of the webs with multiple vertical lines had only one suspension line. Summing these, and data for an additional 31 spiders whose sizes were not noted, the totals are 57.4% of 122 webs had only a single vertical line (47.1% of these lines had two or three attachments to the water); of the 52 webs with multiple vertical lines, 73% had a single suspension line, 25% had two and 2% had three. The mean number of vertical lines in 38 webs with multiple vertical lines attached to a single suspension line was 6.6 ± 3.2 ; the mean number of vertical lines/suspension line in webs with more than one suspension line was similar, 5.9 ± 2.9 .

Spiders on finished webs with multiple vertical lines attached to a single suspension line sometimes rested on the suspension line at the junction with the latest vertical line, holding the vertical line with one leg I and the two ends of the suspension line with its legs IV. In other cases the spider rested on the suspension line beyond the last vertical line, holding the portion of the suspension line to which the vertical lines were attached with one leg I and the other segment of the suspension line with one leg IV.

Webs of mature males

Mature males both constructed and utilized prey capture webs: six different mature males were found feeding on water striders; seven others were found on prey capture webs; and five others were observed constructing nine different prey capture

webs. All male webs had only a single vertical line with sticky balls near the water, though in one case two separate vertical lines were made and then attached together at the top (figure 3B). The construction behaviour of mature males was not distinguishable from that of females (figure 2), except that the males seemed to pause longer between the first ascent and the second descent (at point b in figure 2B). One male failed to make a second descent after a long pause, and thus apparently made a non-functional vertical line lacking sticky silk.

Prey, prey capture and web manipulation

Water striders of at least three species that were common in areas where the spiders were found were captured. Of 85 identifiable prey, all but three were water striders (four other prey were broken into small fragments and could not be identified with certainty, though they also appeared to be water striders). I observed the capture of one of the three exceptional prey, a small flying insect that was trapped in the surface film of the water and drifted into contact with a vertical line; the other two were a moulted spider cuticle and a notonectid bug.

Careful observation of the behaviour of one species of water strider moving in the vicinity of webs indicated that the insects were neither attracted to nor repelled by the sticky vertical lines. They repeatedly passed within 1–2 mm of a line without turning toward or away from it. No vibrations in the water surface were seen to emanate from attachment points to the water.

Prey capture was observed on four occasions. In each case a water strider collided with a sticky vertical line and then remained motionless for 2–30 s. Three of the four spiders remained at the top of the vertical line; the fourth, which had caught a relatively large prey, first shifted the upper attachment of the vertical line with the prey horizontally 2–3 cm, and then moved slowly down the vertical line. In all four cases the water strider suddenly popped up from the water's surface and hung suspended in the air at the lower end of the vertical line. It was not clear whether the water strider's sudden upward movement was due to behaviour of the spider or of the water strider (spiders can produce movements that jerk the vertical line out of the water—see below and figure 5). At least two of the spiders appeared to bite the prey briefly before slowly wrapping it; the spiders' small size and the violent struggles of the water striders precluded certain observations on this point, however.

Only one prey capture was seen in a web with more than one vertical line. This spider's behaviour was similar to that of other *Wendilgarda* species with more typical webs (Coddington and Valerio, 1980; Shinkai and Shinkai, 1997). The spider moved toward the prey along the suspension line, gathering up and carrying along with it several sticky vertical lines that it encountered. Thus when it reached the vertical line with the prey, it brought a bundle of vertical lines to the vicinity of the prey. The spider then walked past the prey on the suspension line and came back. A sudden burst of activity of the water strider caused it to pop up from the water surface, and it immediately contacted and adhered to several of these additional vertical sticky lines.

Although most spiders rested immobile on their prey capture webs, usually at the junction of a vertical line with the suspension line (figure 3C), some, which had single vertical line webs and more or less horizontal suspension lines not far above the surface of the water, dragged the sticky vertical line actively across the water's surface in short bursts of activity. I saw 10 different webs being dragged by six different spiders. In the most active series of dragging, a mature male made 75 drags

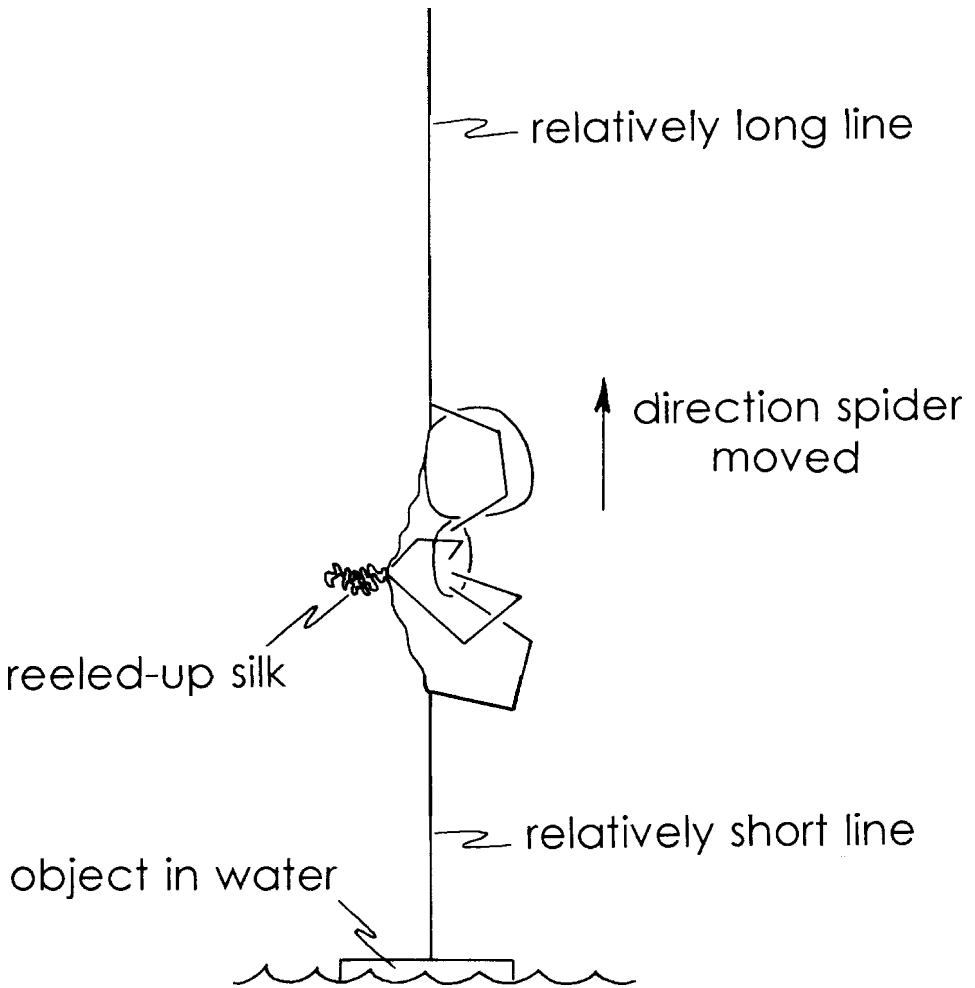
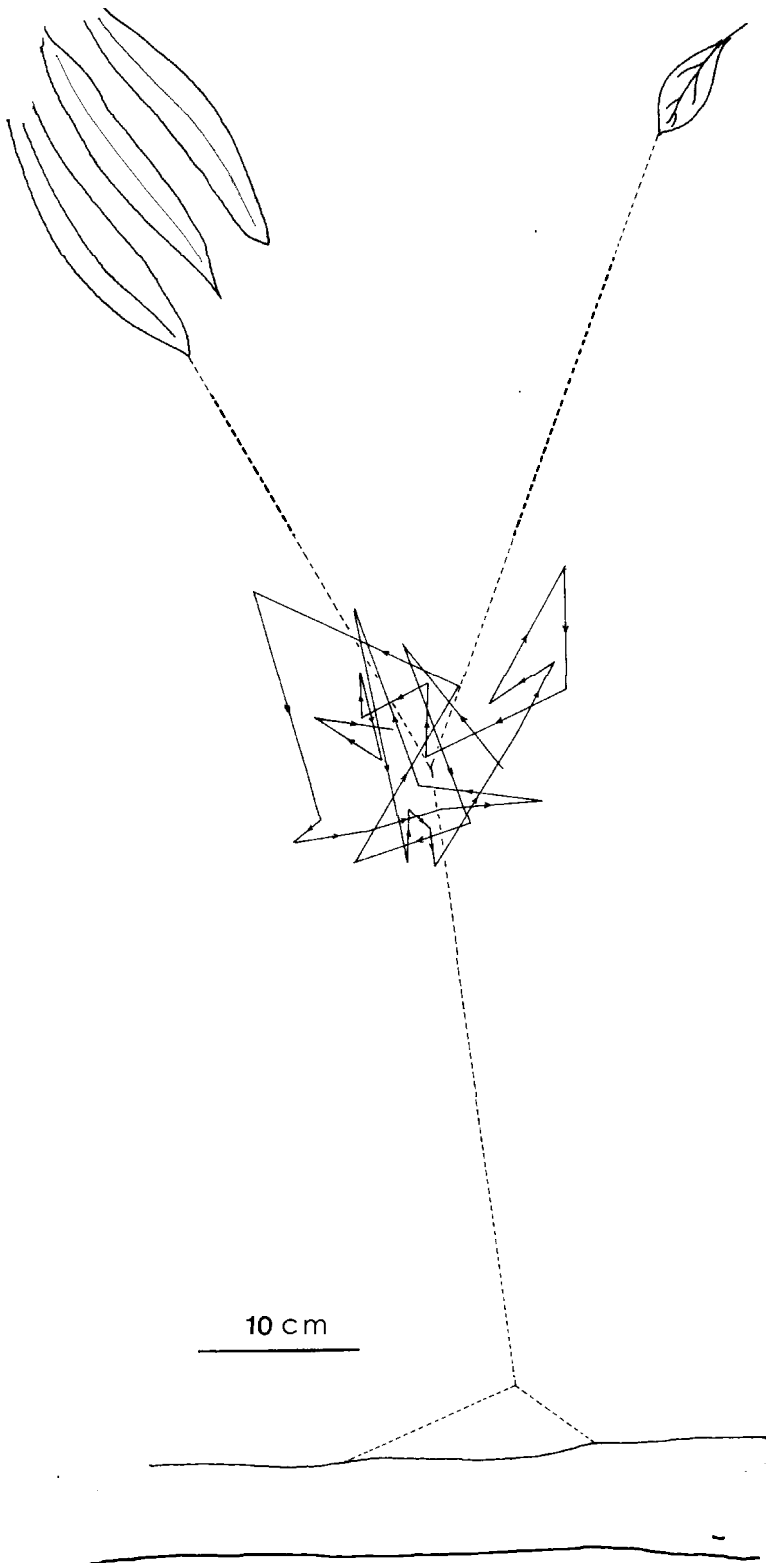


FIG. 5. Probable mechanism used by spiders to jerk objects up out of the water (schematic). The spider first reeled up the line, and thus tensed the entire line. When it then released this silk suddenly, the greater elasticity of the much longer line above the spider caused the spider to be displaced upward (arrow). The momentum of its body produced an upward jerk on the object when the line below its body became tight. This interpretation is tentative, because it was not possible to verify directly that the reeled up line was not broken (as in the drawing).

of 3–20 cm during 62 min (figure 6). The spider appeared to hold the vertical line with one anterior leg while dragging it, but this detail was not confirmed with certainty. In one case the spider moved relatively rapidly (an estimated 10 cm/s) during each drag, then paused nearly immobile for an average of 20–60 s before making the next drag. The dragging movements of a second spider were slower and

FIG. 6. View from above of the movements of a mature male *W. sp.* as he dragged a single vertical line during 25 min of a session lasting 62 min. The dotted lines, attached at four points to supports above the water, mark the suspension lines along which the spider walked and which he broke and reeled up while dragging his vertical line.



more continuous. Still another spider (an immature) made at least seven dragging movements, but then added three more vertical lines to the same suspension line, seven others to a second suspension line, and became immobile.

A second type of web manipulation involved increasing the tension (by reeling in line) and decreasing the tension (by adding additional line) on the vertical line. Decreasing the tension often resulted in increased movements of the lower end of the vertical line across the water surface, as it tended to skate more freely and move farther from directly under the spider.

Microscopic structures of lines attached to the water

A total of eight webs of mature female *W. sp.* were studied under the microscope. The dragline was attached to the centre of a radially arranged set of approximately 30 fine lines (mean = 29.3 ± 5.1 , $N = 5$) (figure 7B); each of these fine lines was apparently thinner and more curled near its tip (figure 8).

There was an attachment disc on the dragline just above the attachment to the water that was continuous with the centre of the water attachment (figure 7B), and immediately above this was an approximately 3 mm section with balls of adhesive material that gradually decreased in diameter moving up the line (figure 7E). The largest balls on the web of one mature female that had been built about 0.5 h previously were about $10 \mu\text{m}$ in diameter. Several lines were visible within many balls flaring away from the central straight line in the ball and then converged on the central line between balls (figure 7A). The maximum number of separate flaring lines was eight: one vertical line had thin lines and six thicker lines; another from another web had two thick, four medium and two thin. It was not possible to determine the number of separate lines in the central line except when they flared away from the central line and each other, and in some balls they flared less than in others. Counts were thus conservative; any line that did not flare away from all others could not be distinguished.

Several millimetres beyond the upper end of the sticky material there was another attachment disc. Beyond this attachment the vertical line generally curled very strongly on itself (figure 7D), as did the suspension line and in contrast with the more or less straight lines below this attachment. In one case in which the sticky line was apparently under very little tension, the central straight line in the sticky region showed a similar tendency to curl, suggesting that it was composed of the same silk (presumably ampullate gland dragline silk). Tightly curled dragline silk also occurred in an orb-weaving theridiosomatid from BCI (probably *Epilineutes*).

The vertical lines in the webs of seven mature females and apparently penultimate nymphs of BCI creek *W. sp.* differed in several respects. Most droplets of liquid were smaller ($2.5\text{--}6 \mu\text{m}$ in diameter) and the droplets extended for a much longer distance along the line (up to about 20 mm). Although the balls near the top of a line were somewhat smaller, on most lines they were much more nearly equal in size along the line, rather than being markedly larger at the very bottom as in *W. sp.*

Attachments to the water in BCI creek *W. sp.* were generally more tangled and had fewer radial lines (figure 7C). Often, radiating lines in the attachment curved back toward the centre and merged in the tangle there instead of ending near the periphery. As in *W. sp.*, their basal portions were thicker. There was always an attachment disc on the central line that was slightly (mean = 0.056 ± 0.037 mm, $N = 15$) above the attachment to the water. There were also sometimes lines flaring away from a straight, central line inside the balls of liquid; the maximum number

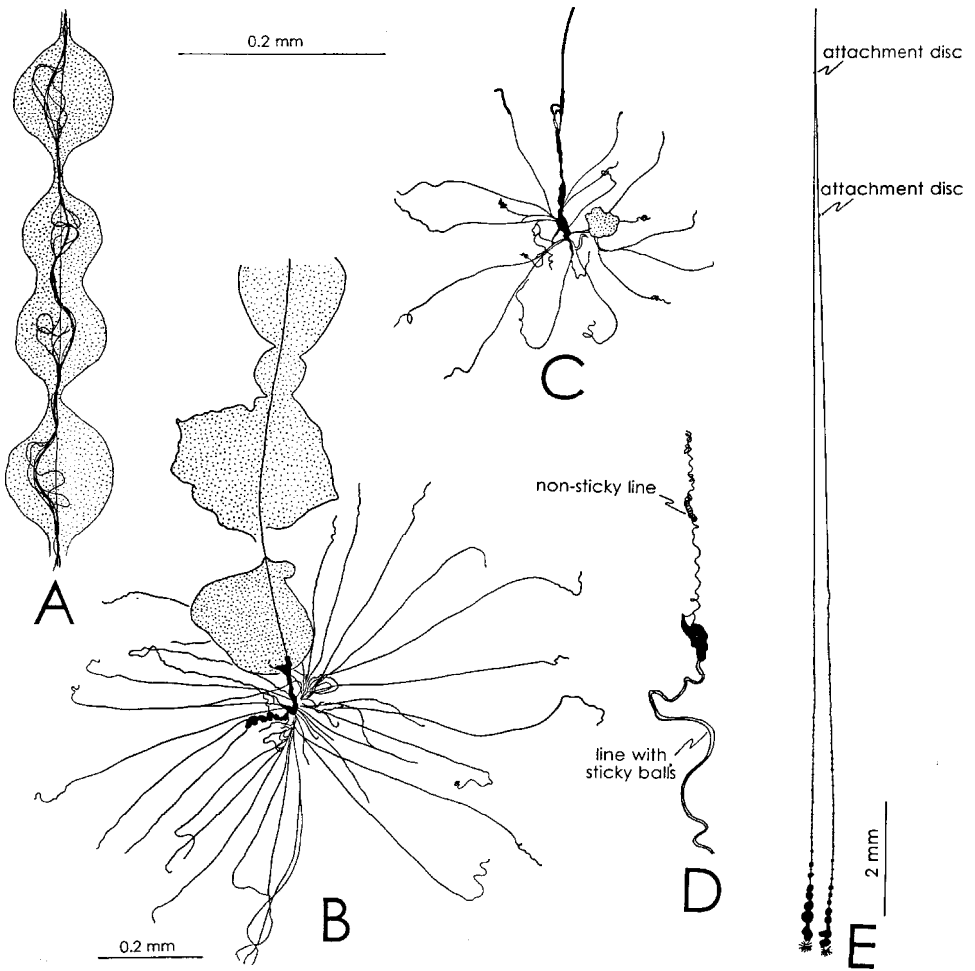


FIG. 7. Microscopic views of silk on slides (stippled = puddles of sticky material; black masses = attachment discs, except for (E) where they = sticky material). (A) Lines of *W.* sp. flare away from central vertical line within masses of sticky material. (B) Attachment of *W.* sp. to water, showing attachment disc (presumed initiation of sticky silk) at bottom tip of vertical line. (C) Attachment of BCI creek *W.* sp. to water, showing attachment disc higher on vertical line and more sparse radial lines. (D) Attachment disc on a slack vertical line of *W.* sp. above section with sticky balls (e.g. d in figure 2), showing greater curliness of non-sticky lines. (E) Puddles of sticky material on a vertical line of *W.* sp., showing strong concentration of material at lower end of the line. Scale for (A), (C) and (D) at upper left.

seen was only four. Flaring lines were much less common than in *W.* sp. They occurred only near the attachment to the water (e.g. figure 7C), and in many lines (eight of 16 checked) they were not seen.

Behaviour of spiders dropped on to water

When mature males and females were allowed to descend on a dragline on to a water surface under a microscope, they sometimes (both sexes) attached a non-sticky line to the water and climbed back up. While the spider was on the surface



FIG. 8. Tips of radial lines of an attachment of *W. sp.* to water, showing how they were progressively thinner near their tips (scale = 0.05 mm).

of the water, it never broke the surface, and the tips of its legs made small downward projecting dimples in the surface film. When a spider was dropped on to the water without descending on a dragline, it walked across the surface with an unusual gait. Legs I and II were repeatedly extended anteriorly and drawn back toward the spider, effectively dragging the spider forward. Each leg IV repeatedly touched the spinnerets rapidly near the tip and then extended rearward in strict alternation. These movements of legs IV resembled pulling silk to wrap prey. During repeated momentary pauses, I confirmed that there was a tight line of silk running from the spinnerets to the tarsus of the leg IV which had most recently touched the spinnerets. This silk did not carry any sticky droplets.

A mature female orb-weaving theridiosomatid (probably *Epilineutes* judging by its web) that was placed on water in the same situation behaved similarly, pulling silk with alternate extensions of her legs IV as she pulled herself forward with legs I and II. This spider did not attempt to attach to the water after descending on her dragline.

Web construction by W. clara

To understand some aspects of the behaviour of *W. sp.*, comparative observations of another *Wendilgarda* species with more typical webs such as *W. clara* are useful. A general description of web construction by this species was given by Coddington and Valerio (1980). Additional observations of 12 webs being constructed by at least six different spiders at the same study site are reported here to provide several more details. Suspension lines were generally in place before vertical line construction began. All vertical lines were made with a double descent–double ascent behaviour similar to that described for *W. sp.*, except that the first ascent reached nearly the top of the vertical line. Most vertical lines on each suspension line were laid in strict order, and all started with the outermost line first (14 of 14 suspension lines). Typically each double descent–double ascent sequence that produced a vertical line occurred near the ‘centre’ of the web (the area where suspension lines converged), and the sticky vertical line was then carried outward to the site where it was attached (11 of 11 suspension lines) (figure 9). The spider then moved back toward the centre before beginning the next vertical line. Often the site where vertical lines were produced was near the site where the innermost vertical line was finally attached. Thus the spider moved shorter and shorter distances outward to attach each successive vertical line to a given suspension line. After attaching a series of vertical lines to one suspension line, the spider then repeated the process on another suspension line. On at least three occasions a spider returned to add one or more vertical lines to the inner portion of a suspension line after having laid vertical lines attached to a different suspension line.

In one case favourable lighting allowed me to see tiny white specks that were probably masses of reeled-up silk. When the spider began the first descent to make a vertical line, it left behind a speck at or very near the junction with the suspension line, which was presumably silk it had reeled up while moving horizontally along the suspension line. The spider stopped short of this speck on its first ascent, and left a second speck on the vertical line as it descended for the second time. The presence of this second speck implies that during the first ascent the spider reeled up the line laid on the first descent (figure 9A). When it reached the suspension line after the second ascent, the spider apparently lengthened the vertical line, as the tension on the line decreased, as the suspension line rose slightly (compare angles of downward deflection of the suspension line in figure 9A, C). The second ascent was relatively jerky; it appeared that the spider pulled out line with its legs IV, but I was not certain. Both specks disappeared when the spider carried the finished vertical line outward after the second ascent to attach it near preceding vertical lines (figure 9D). When it returned along the suspension line to begin the next vertical line, the spider brought another speck with it (figure 9E).

Several substantial variations in the order and technique of placement occurred, even in this small sample of observations. One spider first attached seven vertical lines to a suspension line, then walked out from the central area to the second vertical line it had laid, reattaching several of the vertical lines it encountered along the way, and then walked back in and laid an additional two vertical lines between vertical lines 6 and 7. The second of these was just outward from vertical line 7, and during the first ascent as it laid this line the spider apparently contacted this previous vertical line. Instead of finishing construction of the new vertical line with a second descent, the spider moved back to the central area, and then added four more vertical lines to this same suspension line moving inward from line 7. The first

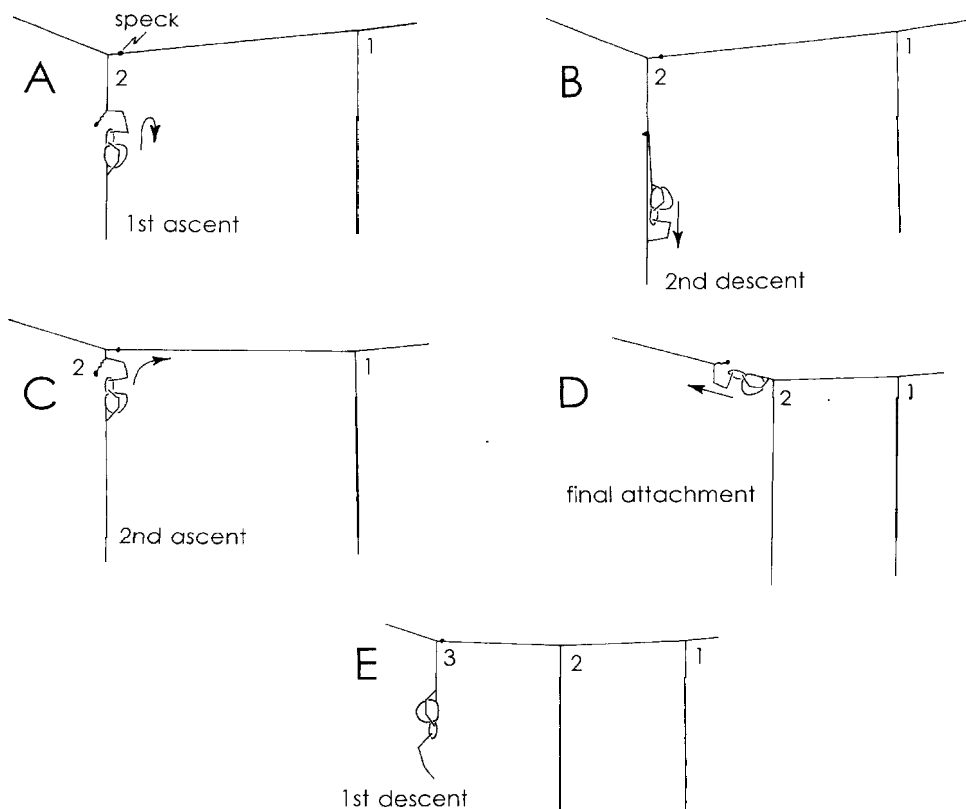


FIG. 9. Stages of the production of a second vertical line (A–D) and the initiation of a third line (E) by *W. clara*. The tight new vertical line (A, B) pulled the suspension line downward as the spider made the second descent; the tension then diminished and the angle in the suspension line became less acute (C; compare with B) as the spider extended the vertical line and then moved along the suspension line toward the previous vertical line (C). The spider apparently reeled up the suspension line as it then moved away from line 2 (D), because the white speck at the top of the new vertical line (dots in A–C) disappeared, and a white speck (presumably the accumulated reeled up silk) moved with the spider to the site where the next vertical line was laid (E). The positions of the white specks on the suspension line with respect to the vertical line in (A)–(C) were not determined by direct observation; they are guesses based on the directions in which the specks moved and new lines were carried.

two of the four were built near the centre and then carried outward, while the third and fourth were made very close to their final attachment sites. A second spider finished adding vertical lines to one suspension line, but then added more non-sticky lines, and then moved out on a second suspension line and repeatedly shifted attachments of non-sticky, more or less horizontal lines at the far end of this line. Finally, it attached several sticky vertical lines to this suspension line. A third spider shifted attachments of non-sticky lines at the far end of a suspension line after laying one vertical line attached to this suspension line, and then laid several other vertical lines.

The finished webs of eleven mature and penultimate *W. clara* differed from those of *W. sp.*, and resembled those described by Coddington and Valerio (1980). All had either three (73%) or four (27%) suspension lines. The mean number of vertical

lines/suspension line was $7.1 + 3.1$. Suspension lines were relatively short (mean = $8.8 + 4.6$ cm, $N = 19$), and were near the surface of the water (mean = $3.6 + 1.2$ cm where the spider hung, $N = 8$).

Discussion

Comparing webs of W. sp. and other Wendilgarda

The diversity of web forms now known in the six studied species of *Wendilgarda* is unparalleled in any other genus of orb-weaving spiders. The typical webs of several species, including *W. clara*, and *W. mexicanus* Keyserling (Coddington and Valerio, 1980), *W. galapagensis* Archer (Eberhard, 1989), Japanese *W. sp.* (Shinkai and Shinkai, 1997) and BCI creek *W. sp.* have multiple sticky vertical lines that are attached to stream surfaces. These webs capture both flying insects (which are especially common close to the surface of the water—Buskirk, 1975; J. A. Coddington, personal communication), and insects walking on or trapped in the water surface (Coddington, 1986; Eberhard, 1989a; W. Eberhard, unpublished observations of *W. galapagensis*). The webs of *W. sp.* differ from those of the other species in having as few as only one vertical sticky line and one suspension line, both of which are usually much longer and often much higher over the water than those of other species.

Judging by the fact that *W. sp.* fed nearly exclusively on water striders, their simplified webs represent a specialization for capturing insects on the water surface rather than those flying just above it. The concentration of adhesive at the bottom of vertical lines near the attachment to the water (figure 7E), and the frequent construction of webs with multiple sticky lines attached to the same vertical line with their sticky lower ends near together (e.g. figures 3A, 7E) are probably adaptations for capturing relatively large and vigorous prey like water striders. The Japanese *W. sp.* also shows a tendency to place sticky silk on only the lower one- to two-thirds of each vertical line, but did not attack water striders that occurred in the same habitat (Shinkai and Shinkai, 1997). The fact that the same individual spider of *W. sp.* can make several webs in less than an hour indicates that their webs are 'cheap' in terms of the spider's silk reserves, as compared with orb webs that apparently often use up a large fraction of the spider's silk gland contents (Witt *et al.*, 1968; Eberhard, 1989b).

The construction behaviour of *W. sp.* differed from that of other *Wendilgarda* in several respects. Although vertical lines were made with double descent—double ascent behaviour seen in all *Wendilgarda* species observed to date (below), the relative distances moved differed: the second descent reached near the bottom end of the line as in the Japanese *W. sp.* instead of stopping short as in *W. galapagensis* (Eberhard, 1989a). The length of the sticky portion produced during the second ascent was shorter than in other *Wendilgarda* species (Eberhard, 1989a; Shinkai and Shinkai, 1997; above).

There was probably a subtle difference in the behaviour employed by *W. sp.* to produce webs with multiple sticky vertical lines when compared with the construction of similar webs by *W. clara*, *W. galapagensis* and the Japanese *W. sp.* (Eberhard, 1989a; Shinkai and Shinkai, 1997; above). Instead of walking horizontally along the suspension line and dropping to the water below to make successive vertical lines, *W. sp.* sometimes spaced successive vertical lines by adding additional silk to the suspension line, breaking it and paying out new dragline after making each vertical

line (figure 4A). Thus, unless this detail was missed in observations of the other species (I can be certain it was not only with *W. clara*), an apparently homologous structure (multiple vertical sticky lines attached to a suspension line) was built utilizing non-homologous behaviour (see Hansell, 1984; Eberhard, 1990a; Wenzel, 1992; Stuart and Hunter, 1998 for discussions of the difficulties of determining behavioural homologies).

Judging from the details of lines observed in the microscope, *W.* sp. also differed, at least from BCI creek *W.* sp., in that the attachment to the water had more radial lines. The attachment to the central line (presumably the initiation of the sticky line made during the second ascent—point c in figure 2) was nearer to the attachment to the water, and the baselines of the sticky silk (presumably those lines which flared from the central line within droplets of sticky material) were laid under much less tension (and thus flared much more often). These details may also represent derived traits of *W.* sp. that function to improve capture of water striders, but more observations of webs of other species are needed.

Active searching for prey

Although phylogenetic relations within the genus *Wendilgarda* remain undetermined, it is likely that the greater simplicity of the webs of *W.* sp. is a derived character. This is because individuals of this species also sometimes make webs resembling typical *Wendilgarda* webs, and because they employ prey attack behaviour in these webs that includes the same, otherwise unique web modification behaviour ('snow-plowing' of Coddington and Valerio, 1980; see also Shinkai and Shinkai, 1997) that is presumably correlated with this web design as it brings multiple sticky lines into the vicinity of the prey. As others have noted (e.g. Kaston, 1964; Eberhard, 1990b), web reduction has occurred many times independently in the evolution of spiders and is often associated with more active web manipulation to capture prey. The webs of *W.* sp. are unique, however, in that they move substantial distances and are sometimes actively moved by the spider *prior* to the arrival of prey in the near vicinity. These webs thus 'search' actively for prey. The adaptive significance of both the low number and the extraordinary length of vertical lines in some *W.* sp. webs (compared both with other *Wendilgarda* species, and with the size of the spider itself) may be to increase the area that is covered when the tip of the vertical line skates on the water surface. This speculation is supported by the fact that the suspension lines of *W.* sp. webs with multiple vertical lines were closer to the water surface (table 1).

The idea that movements of the sticky vertical line are advantageous was supported by observations of spiders actively dragging sticky lines across the water surface. Probably the mobility of attachments to the water surface even when spiders did not move resulted from the combination of several factors: small movements in the wind of the leaves and branches to which the spider's non-adhesive lines were attached above; low tensions on the vertical lines; movements of the water itself; and the elasticity resulting from the substantial length of the line between the supports above and the water below. The tightly curled configurations that non-sticky lines often assumed when they were slack (figure 7D) may increase this elasticity. The points of attachment of vertical lines to the water in the webs of other *Wendilgarda* such as *W. clara* also move in the surface film (Coddington and Valerio, 1980), but the vertical lines of these species are quite short (table 1), and are thus only free to move short distances.

A second, non-exclusive possible advantage of the relatively long vertical and suspension lines of *W. sp.* is an increase in elasticity and thus an increase in the ability to absorb the impact of prey. This idea is also supported by shorter lengths of vertical lines in webs with multiple vertical lines, since the multiple vertical lines could also provide increased ability to stop and retain prey. Greater elasticity would also improve the web's ability to adjust to momentary reductions in water level without pulling free of the water surface. This last factor could be important in Gatun Lake due to the frequent brief changes of water level caused by passing ships.

The vertical lines were apparently not attractive to the water striders. Thus web reduction in this species is not associated with the ability to attract prey as in some other spiders (Hansell, 1984).

The striking arcs that *W. sp.* spiders described as they descended during web construction (figure 1) have not been reported in any other *Wendilgarda* species. They probably function as exploratory movements to help the spider avoid making a web at a site that lacks enough open space. The long vertical line can only skate freely on the water if there are no objects in the space between the spider and the water. Such exploration would be less crucial in other species of *Wendilgarda* with webs close to the water surface.

Behavioural homologies

Coddington and Valerio (1980) suggested that the non-sticky suspension lines and the sticky vertical lines of *Wendilgarda* webs are homologous with, respectively, the radii and sticky spirals of theridiosomatid orbs. Several types of data support these homologies. The fact that suspension lines generally converge on a central area of the web, that they are usually built before the sticky lines are begun, and that they are non-sticky and support regular arrays of sticky lines, all favour the idea that they are homologous with radii. Homology of vertical lines with sticky spirals in orbs is supported by the adhesive nature of at least part of the vertical lines, their apparently great extensibility (Coddington and Valerio, 1980), the pulling behaviour of the spider's legs IV during their construction (Eberhard, 1989a, above), the folding of lines within the balls of sticky material (figure 7A), and the tendency to build the vertical lines from the periphery inward in the web (Eberhard, 1987) (see Witt *et al.*, 1968; Eberhard, 1982 on other orb weavers).

One unique building technique that is shared by all *Wendilgarda* species that have been observed in sufficient detail is the production of an 'extra' non-sticky line that is attached to the surface of the water preceding the production of each segment of sticky line. Each sticky line in a finished web was a compound line, composed of both a sticky line and a previously laid non-sticky line or lines, so this line is not easily homologized with any line in orb webs. Such double descent-ascend behaviour does not occur in water attachment behaviour in the anapid *C. lyugadinus* (Shinkai and Shinkai, 1988), or in the theridiid *T. bergi* (Xavier *et al.*, 1995). It is such a consistent part of attaching lines to the water in *Wendilgarda* that it seems likely that it arose before or during the evolution of the ability to attach sticky lines to the water. Although the description of *W. galapagensis* behaviour is not entirely clear on this point (Eberhard, 1989a), it appears that at least the upper portion of the vertical sticky lines in water and low land webs may not be doubled over a non-sticky line as in *W. sp.* These compound lines may thus not be strictly homologous within the same genus.

Although the first descent–ascent behaviour pattern occurs during the construction of sticky lines, perhaps it is derived from the attachment of frame lines to water surfaces as in the theridiosomatid *Epilineutes globosus* (Xavier, 1995). Attachments to the water surface of non-sticky drag lines also occurs in *W. sp.*, and involve only a single descent and ascent as in *E. globosus*. The morphology of the water attachment in *E. globosus* (Xavier, 1995; Xavier *et al.*, 1995) is very similar to that of *W. sp.* Both, in fact, are similar in general appearance to typical attachments to solid substrates (e.g. Schütt, 1996), but differ from the water attachments of *T. bergi* (Xavier *et al.*, 1995). In addition, *E. globosus* sometimes attaches several adjacent lines to the water; the upper portions of these lines sometimes merge as in the vertical lines of *W. sp.*, but they always remain separated at the tips where they are attached to the water, just as in *W. sp.* (Xavier, 1995). Xavier (1995) mentions the possibility that the thin disc of material associated with the radial lines of the attachment was responsible for this lack of fusion, but I was unable to see such material in water attachments of *W. sp.* The derived nature of building webs attached to water in *E. globosus* is indicated by both outgroup comparisons with other genera of theridiosomatids, and by ontogenetic changes toward more webs attached to the water in older spiders (Xavier, 1995) (a trend that also occurs in the anapid with aquatic webs—Shinkai and Shinkai, 1988). Taken together, these data imply that behaviour patterns that evolved in separate contexts (frame construction and sticky spiral construction) in common ancestors of *Epilineutes* and *Wendilgarda* have been recombined in *Wendilgarda*. Reorganization of behaviour patterns occurs in many other species (Hansell, 1984 and references therein).

A second derived building technique that may be unique to *Wendilgarda* among other theridiosomatids and other orb weavers in general is dragging a newly built vertical sticky line from a central location toward the periphery of the web. This movement resembles the movement of an orb-weaving theridiosomatid prior to attaching a segment of sticky spiral, except that the ‘radial’ line (the suspension line) is reeled up and replaced as the spider moves instead of being left intact. Carrying vertical lines is very similar to the ‘snow plow’ attack behaviour in several species of *Wendilgarda* (Coddington and Valerius, 1980; Shinkai and Shinkai, 1997; above). This is thus a second possible case of a behaviour pattern that has been shifted to a new context, though in this case the direction of derivation is not known (from web construction to attack, or *vice versa*). Dragging sticky lines attached to the water surface also occurs in the anapid *C. lyugadinus*, though over relatively shorter distances (Shinkai and Shinkai, 1988). In this context, the tendency to return to the central area before initiating the next vertical line, as occurs in *W. clara*, is derived with respect to initiation of the next vertical line near the site of the innermost previous vertical line, as occurs when orb weavers produce sticky spiral lines. In *W. sp.* the technique of dragging a finished vertical sticky line has been adopted to function in still another context—dragging finished vertical lines across the water surface to contact prey. This behaviour is thus probably partially homologous with sticky spiral construction in orb weavers.

One detail that was similar in all species was that during vertical line construction the spider seldom touched the innermost previously laid vertical line prior to making the final attachment of the vertical line to the suspension line. The often very uniform spaces between adjacent vertical lines were thus presumably the result of the spider keeping track of the distances it moved along the suspension line (or, in the case of *W. sp.*, the length of dragline it added to the suspension line—see figure 4).

This kinesthetic sense, documented experimentally in the tetragnathid *Leucauge mariana* (O. Pickard-Cambridge) (Eberhard, 1988), probably also occurs in other theridiosomatids that build orb webs (Eberhard, 1982).

Behavioural flexibility

The large intraspecific variability in the behaviour used by *W.* sp. to build webs is typical of other species in this genus (Eberhard, 1989a; Shinkai and Shinkai, 1997 on order of vertical line placement; descriptions of *W. clara* above). Some aspects of this variation are especially impressive because they involve behavioural changes that have apparently never been reported in any other of the more than 150 species which have been observed (Witt *et al.*, 1968; Eberhard, 1982), which are widely distributed taxonomically among the many thousands of species of five araneoid families of orb weavers (Coddington and Levi, 1991; Griswold *et al.*, 1998). For instance, orb weavers are very strict regarding the order in which non-sticky and sticky lines are produced: first the scaffold of non-sticky lines is finished, then all sticky lines are laid uninterrupted by placement of further non-sticky lines. In *W.* sp., *W. galapagensis* and *W. clara* spiders sometimes interrupted production of sticky lines to add to the scaffold of non-sticky lines, then resumed sticky line production. The only other exception to this strict order of non-sticky and sticky lines that I know of occurs in *Araneus atriastula* (Forster and Forster, 1985). Other 'rules' of orb weavers that were often violated by all three *Wendilgarda* species were to refrain from further exploration and production of spanning lines once construction of the definitive web has begun, never move outward along a radius past the innermost sticky line during sticky line construction, and never alter the position of a sticky line once it has been produced.

Striking flexibility in construction behaviour even occurred in successive webs of the same individual of *W.* sp. For example, one spider employed different behaviour patterns to achieve the same end in successive webs. In the first web it laid the first vertical line near the left end of the suspension line, and then laid subsequent vertical lines to the right. In the next web it laid the first vertical line near the right end of the suspension line, but then carried it to the left end, attached it, and then laid subsequent vertical lines to its right as before. This variability echoes the even higher level of intraspecific variability in *W. galapagensis*, in which three different basic web designs occur (Eberhard, 1989a), and the Japanese *W.* sp., which builds both typical *Wendilgarda* webs attached to the water, and theridiid-like webs with multiple sticky lines attached to a stone and converging above (Shinkai and Shinkai, 1997). Perhaps the simplicity of the web forms of these *Wendilgarda* species is related to this extravagant variation (W. Eberhard, in preparation).

The especially simple web forms of *W.* sp. may be related to the otherwise unusual and perhaps unique observation of a mature male in an orb-weaving family building his own adhesive prey capture web. The only other species in which mature males have been found to make adhesive prey capture webs is the tangle-web builder *Comaroma simonii* Bertkau, which has been variously classified as an anapid, a theridiid and an erigonid (Kropf, 1990, 1997). Perhaps significantly, the webs of this species also have relatively small amounts of sticky silk (Kropf, 1990). Non-sticky webs of mature males, on the other hand, have been seen in several other groups. Some mature male theridiosomatids (e.g. *Theridiosoma gemmosum* (L. Koch), *Epeirotypus* sp.) make simple tensed arrays of non-sticky lines that appear to be stripped-down versions of radii and tension lines of orbs, and use them

defensively to spring away when in danger (Coddington, 1986; W. Eberhard, unpublished). Similarly, mature males of *Mecynogea* spp. (Araneidae) and some *Uloborus* and *Philoponella* species (Uloboridae) make small sheets of non-sticky lines (Eberhard, 1977 and unpublished), presumably to capture prey. Mature males of the bolas spider *Mastophora dizzydeani* Eberhard apparently capture prey, judging by the spines on their anterior legs (e.g. Eberhard, 1980), but again they presumably do so without producing sticky silk. The not uncommon observation of web robbery by mature males of some araneids and tetragnathids (Eberhard *et al.*, 1978; W. Eberhard, unpublished on *Leucauge mariana*) argues that mature male orb weavers of a number of species can often benefit from capturing prey. Perhaps male *W.* sp. have turned an important evolutionary corner.

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