Niche expansion in the spider *Wendilgarda galapagensis* (Araneae, Theridiosomatidae) on Cocos Island

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Abstract: *Wendilgarda galapagensis,* a species endemic to Cocos Island, shows an unusually wide variation in habitat choice, web design, and construction behavior. Differences between *W. galapagensis* and close relatives are probably derived rather than vestiges of characters of a common ancestor. Cocos Island has an impoverished fauna, and the derived characters of *W. galapagensis* may have evolved in response to reduced interspecific competition, reduced predation, or increased intraspecific competition.

Key Words: *Wendilgarda*, spider webs, Cocos Island, competition, niche expansion.

Niche expansions are known to occur on isolated, depauperate oceanic islands, especially in birds (VanValen 1965, Diamond 1970, MacArthur *et al.* 1972, Grant 1972, 1986, Lister 1976, Werner and Sherry 1987). The present report describes a particularly dramatic case of niche expansion in an invertebrate, the web-building spider *Wendilgarda galapagensis* Archer, which is endemic to Cocos Island in the eastern Pacific (Archer 1953).

A major portion of a web-weaving spider's predatory behavior is manifested in habitat choice, web designs and construction behavior. By studying these characters, one can quickly establish many basic aspects of such a spider's predatory behavior. The webs of at least three mainland species of the approximately 15 known species of *Wendilgarda* (*clara, mexicana,* and an undescribed species) are all built exclusively over the surface of forest streams (Coddington and Valerio 1980). Webs of the entire family Theridiosomatidae are known only from forested or otherwise shady, protected sites (*e.g.* culverts) (Coddington 1986a). All known *Wendilgarda* webs consist of a series of more or less vertical sticky lines, each attached at its lower end to the surface film of water in a stream, and above to one or more approximately horizontal non-sticky lines (Fig. 1). (Coddington and Valerio 1980, Coddington 1986a, W. Eberhard unpub.). This extraordinary design undoubtedly evolved from a more typical orb, as *Wendilagarda* is clearly a derived member of the orb-weaving family Theridiosomatide (Coddington 1986a). This note shows that the webs and building behavior of *W. galapagensis* differ from those of other *Wendilgarda* in ways which suggest that this species occupies an unusually wide niche on Cocos Island.

MATERIAL AND METHODS

Between 2 and 7 Dec. 1987 I observed in the field at least portions of the construction of 29 webs on land and 11 over water, and a total of 100-200 finished webs on land and 20-50 webs over water. Most behavioral observations were made around 5 AM and 4 PM, when bursts of building behavior occurred. Spiders building in darkness were illuminated with red light. Unless otherwise noted, behavioral observations refer to mature or penultimate individuals; web designs of younger immatures did not differ appreciably from those of larger individuals. Sticky lines were distinguished from non-sticky lines by their covering of small balls of adhesive which made them easier to see. Spiders collected near water, in short grass, and in forest away from water were identified by comparing male pedipalp morphology with that of the type specimens. All had similar palp morphology. Voucher specimens will be deposited in the Museum of Comparative Zoology, Cambridge, Mass. and the Museo de Zoología of the Universidad de Costa Rica.

RESULTS

Websites. Webs of *W. galapagensis* were found in a wide variety of sites: over and along the edges of Rio Genio and smaller tributaries which ran through forested areas; in vines and vegetation on and near large tree trunks in wet forest from 3-150 m up on the steep slopes of the island; in the upper parts of the 1-3 m tall grass in forest at low elevations; and in low (10-15 cm) grass and small portions of bare ground in open clearings both at about 5 m and on ridges at about 200-300 m elevation. In fact, spiders occurred in all non-coastal areas on the island where I searched for them. The most heavily populated sites along streams and in short grass in the open had densities of up to 10-40 individuals/square meter.

Web Designs. Webs over water. All webs over water ("water webs") were similar to webs of other *Wendilgarda* species. They had one to six approximately horizontal lines 1-15 cm above the water's surface which were attached at their outer ends directly to the substrate (a rock, stick, etc.). Most horizontal lines supported a series of short, closely spaced, vertical sticky lines attached to the surface of the water (Fig. 1). The horizontal nonsticky lines converged in a central area, and often one or more non-sticky lines extended obliquely upward in this area. The spider usually rested in the central area, facing downward.

Webs over land. Webs over dry land ("land webs") consisted of long sticky lines attached at one end to non-sticky lines which ran directly to the substrate, and at the other to a sparse central network of non-sticky lines where the spider rested (Figs. 2-4). Orientations and lengths of sticky lines varied according to the website. Most sticky lines in webs built close to the ground ("low land webs") were similar to those of water webs in being close to vertical (Fig. 2), but sticky lines were fewer and longer than those in water webs (Table 1). Webs higher in vegetation ("high land webs") differed in having even fewer and longer sticky lines which radiated in a variety of directions from the central area (Figs. 3-5, Table 1).

TABLE 1

Comparison of webforms of water, low land, and high land webs of W. galapagensis *(averages, standard deviations, and ranges are given, with sample sizes in parentheses). All three types of website differed significantly in both variables ($p > .001$, Mann-Whitney U tests)*

Website	Mean Number sticky lines/web	Mean lengths of sticky lines (cm)
Water	23.2 ± 12.4,6–41 (11)	1.2 ± 0.3, 0.8–2.0 (71)
Low land	13.5 ± 3.4,8–21 (24)	7.6 ± 2.3, 3–15 (151)
High land	5.4 ± 2.4, 1–12 (39)	13.0 ± 3.8, 5–26 (125)

Web construction. The first construction stage consisted of laying and replacing non-sticky lines, and shifting connections between them; some of these lines eventually formed horizontal lines in the finished web. Spanning lines (Eberhard 1987a) were launched, and sometimes quick, apparently exploratory descents were made to the substrate below, followed by removal of the dragline as the spider climbed back to where it had started. This apparently exploratory activity began an hour or more before web construction proper, and was often interrupted by pauses of up to 30 minutes or more.

The spider began sticky line construction by walking away from the central area on a preexisting non-sticky line, or descending on a new line. In all cases the spider executed a series of three 180° turns before it began laying sticky silk (Fig. 6). In building water webs both the first and third attachments made during this maneuver (*a* and *c* in Fig. 6) were to the water (this was ascertained by noting the "pimple" in the surface film that formed where a line was attached to it), and the distance *a-b* relatively short. In land webs the distance *a-b* was always longer than *b-c*, and was in some cases longer than the entire sticky portion of the line. In some cases in land

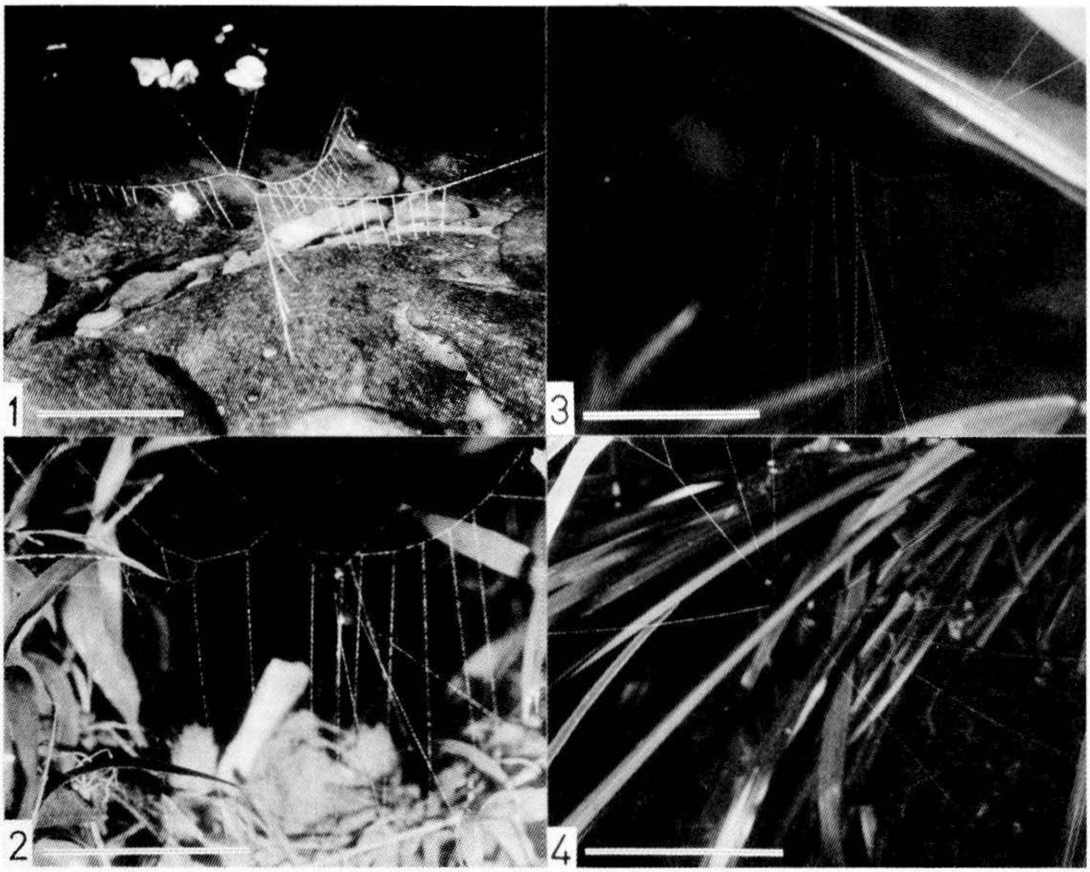
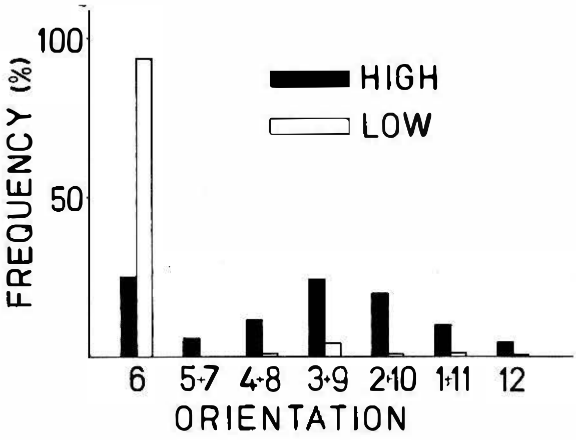
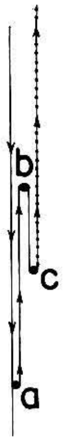


Fig. 1. "Water web" of *Wendilgarda galapagensis* built over the edge of a stream (scale = 10 cm). The short vertical lines to the water surface were sticky, while all others were non-sticky.
Fig. 2. "Low land web" of *W. galapagensis* built in 10-15 cm tall grass in a clearing near Rio Genio (scale = 10 cm).
Figs. 3 and 4. Two "high land webs" of *W. galapagensis* built 1.8 m over dry land in forest on Cocos Island (scale = 10 cm). The two webs were on the same plant, and less than .5 m apart.

webs attachment *a* was to the substrate, but in others it was to the broken end of a line the spider had reeled up as it moved away from the central area. In all webs the spider then laid sticky line by pulling it out with alternate strokes of its hind legs as it returned from *c*, reeling up its dragline, to where it had started. It apparently lowered the tension on the sticky line by pulling several additional strokes with its hind legs (Eberhard 1981) when it reached the starting point, then attached the sticky line there.

Although the designs of water webs were similar to those of low land webs in having series of vertical sticky lines attached to a few horizontal non-sticky lines, the sequences in which sticky lines were added at the two types of websites were surprisingly different (Fig. 7). All but two of 173 vertical sticky lines observed being built in 8 water webs were laid starting with the outermost sticky line first and working inward in strict order (Fig. 7A), and the central area of the web was not visited until the entire series of sticky lines on a horizontal line had been laid (in one of the two exceptional cases a spider interrupted a series of lines to go to the central area, then immediately returned and finished the series). In contrast, only 5 of 47 vertical sticky lines observed being built in 6 low land webs were laid just inward of the preceeding sticky line and without an intervening visit to the central area. Spiders usually returned to the central area of these webs after each sticky line was laid (40 of 47 cases); the order of sticky lines showed no clear pattern (Fig. 7B).





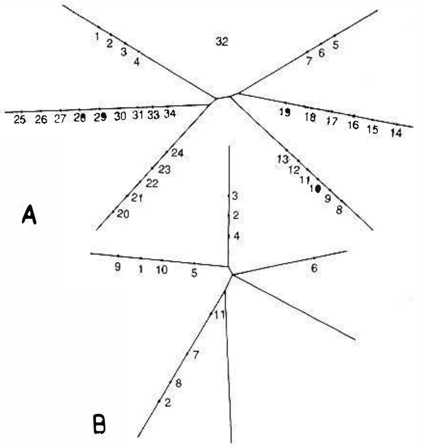


Fig. 5. Distribution of orientation of sticky lines in land webs with respect to gravity (6: 00 is straight down, 9 and 3:00 horizontal, etc.). Differences between high and low land web distribution are significant ($p > .001$ with Chi Squared Test).

Fig. 6. Schematic representation of the sequence of events at the start of production of a sticky line. The spider moved away from the central area of the web, reeling up the line and replacing it with its non-sticky dragline. It attached (large dot at a), turned and climbed part way back to attach to its dragline and turn back again (b); then it went back down a short distance and attached and turned once again (c), then began laying sticky line (line with dots) as it returned to the place where it had started. Spiders probably broke and reeled lines in moving from a to b to c (they generally broke and reeled lines wherever they moved in their webs), but these details were not verified by direct observation.

Fig. 7. Schematic representation of order of vertical sticky line placement in a water web (A) and a low land web (B).

The order of addition of sticky lines to high land webs was, if anything, even less strictly organized. Spiders always returned to the central area after each sticky line (> 50 cases in > 8 webs). During pauses at the central area between laying sticky lines spiders broke and reattached non-sticky lines, initiated spanning lines, broke and shifted attachments of previous sticky lines to non-sticky lines, descended up to 20-30 cm on draglines and then climbed quickly back up to the point of origin without removing the line just laid, and broke and shifted attachments of dry lines to the substrate. There was no clear order to sticky line production in high land webs. On more than five occasions I saw that a spider which started away from the central area on the inner non-sticky portion of a sticky line turned back when it encountered sticky silk, then moved out another line to lay a sticky line, suggesting that the spiders themselves were not certain where they had already laid sticky silk.

An inadvertant experiment showed that individual *W. galapagensis* probably do not specialize in particular web designs in the way that Cocos finches (*Pinaroloxias inornata*) specialize in particular types of foraging (Werner and Sherry 1987). One morning a heavy rain produced extensive puddles in the short grass habitat. The spiders there, which had consistently made typical low land webs as described above, spun typical water webs (5 cases observed), using typical water rather than land web construction behavior (2 individuals observed) when attaching to the surfaces of the puddles.

DISCUSSION

While *W. galapagensis* builds water webs essentially identical to those described for other *Wendilgarda* species (Coddington and Valerio 1980), it differs in also building webs away from water and in open habitats, in making a variety of additional webforms, and in performing a number of different construction behaviors (e.g. return to central area after each sticky line, replace non-sticky lines with sticky lines; not attach sticky line directly to substrate but to a non-sticky line which is attached to the substrate). There are several reasons to believe that these differences are newly evolved, derived characters, and thus that they may have been favored by unusual selective conditions associated with Cocos Island.

It is highly likely that the use of highly exposed websites is a derived character, since other *Wendilgarda* species as well as those in other, less derived genera of Theridiosomatidae seem to be limited to more protected sites (Coddington 1986a).

The position of *galapagensis* within the genus *Wendilgarda* is not yet determined, and other theridiosomatids build webs over land, so it is not at first obvious whether or not *galapagensis* land webs are derived. Details of *galapagensis* land web designs and building behavior suggest, however, that they are secondarily derived. The probable primitive webform for theridiosomatids is an orb (Eberhard 1982, Coddington 1986b). Several aspects of water webs, includingthe strict order of construction and the even spacing of sticky lines in *galapagensis* water webs, and lack of frequent returns to the central ("hub") area are more similar to sticky spiral construction in orbs (*e.g.* Tilquin 1942) than are the less organized sequences and frequent returns in high land webs. The interspersal in land web construction of other activities such as spanning line production and readjustments of dry line attachments between construction of sticky lines is also clearly derived with respect to undisturbed orb construction behavior in other theridiosomatids and araneoids, where sticky line production always continues uninterrupted by other activities once it has begun (Tilquin 1942, pers. obs. of the approximately 120 species in six families mentioned in Eberhard 1982, 1987b).

The reason why sticky line placement is less rigidly organized in land webs may be related to the difficulty of finding appropriate attachment sites on the substrate below the web. Spiders on webs over water have essentially an uninterrupted plane surface to which they can make attachments, while on land the substrate below low webs is always much less regular. Quick descents and reascents that did not result in new lines were seen frequently in land web construction, and are probably exploration behavior designed to inform the spider about objects below the web.

It seems probable that the ancestors of *W. galapagensis* began building webs away from water, and then evolved new construction behaviors and web designs appropriate for these sites. What aspects of the environment on Cocos Island could have favored this change in habitat? The three most probable (and nonexclusive) hypotheses which come to mind are reduced interspecific competition, reduced predation and increased intraspecific competition. There is some experimental evidence that at least weak or intermittent interspecific competition (both exploitive and interference) occurs between pairs of orb-weaving species at very high densities (Spiller 1984a, 1984b), but in several other cases interspecific competition could not be demonstrated (Wise, 1981, 1983, Horton and Wise 1983 –see Wise 1984). These studies tested the effect of only pairs of species on each other, however. Judging both by searches for other species of orb weavers (10 spp. on Cocos as compared with 40 spp. after a more or less similar search in lowland forest on the mainland of Costa Rica at La Selva – W. Eberhard , unpub.), and by the generally depauperate assemblage of arthropods on Cocos (Hogue & Miller 1981), Cocos probably "lacks" a variety of web-building species. It seems safe to say, especially if the ancestor of *W. galapagensis* arrived at Cocos before the other common orb-weaving species did, that the ecological vacuum it experienced there in terms of possible competition from other species of web weavers may have been very appreciable.

Cocos is undoubtedly also depauperate with respect to potential predators of *W. galapagensis.* For instance, only seven species of land birds occur there, and hummingbirds, which are known to capture theridiosomatids (W. Eberhard, unpub.) are absent. Reduced predation could have allowed expansion to nonaquatic websites. Intraspecific competition, accentuated at high population densities such as those that now occur in some parts of the island, could also have favored spiders building away from water.

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RESUMEN

La araña *Wendilgarda galapagensis* es endémica a la Isla del Coco. Esta especie construye telas en una mayor variedad de habitats que otras especies de su género y familia. El diseño de su tela y el comportamiento de construcción también son más variables de lo típico en otras especies del género. Estas diferencias son aparentemente derivadas –es decir parece que surgieron con la línea evolutiva particular de esta especie, en lugar de ser características de un ancestro de todo el género. Por lo tanto se puede deducir que probablemente representan ajustes a las condiciones bióticas particulares de la Isla del Coco. La variedad de la fauna de la Isla es pobre, tanto en otras arañas como en depredadores potenciales de *W. galapagensis*. Las diferencias que esta especie muestra con las otras especies del género podrían haber resultado de una falta de competencia interespecífica, una falta de depredación, y/o una mayor competencia intraespecífica en la isla.

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