

Silk Spinning Behavior and Domicile Construction in Webspinners

J. S. Edgerly,^{1,2} J. A. Davilla,¹ and N. Schoenfeld¹

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*Analysis of spinning and of silk domiciles revealed similarities and differences for three species of embiid: *Antipaluria urichi* (Saussure), *Pararhagadochir trinitatis* (Saussure), and *Oligotoma saundersii* (Westwood). Each exhibited similar routines while spinning; they positioned the silk by touching the substrate with either front tarsus and by moving the leg to the next position, with many silk strands issuing forth at each step. Reinforced pathways developed as they spun while traveling from diurnal retreats and nocturnal foraging zones. Frass from the interior of their domiciles was spun into the silk. *O. saundersii* was unique in that it plastered its silk with gathered materials. Analysis of field colonies of *P. trinitatis* and *O. saundersii* showed that, like *A. urichi*, adult females share their silk with offspring and, often, with other females.*

KEY WORDS: Embiidina; Embioptera; webspinners; arthropod silk; silk spinning.

INTRODUCTION

Embiids (Order Embiidina or Embioptera) live within the confines of spun silk except during brief dispersal flights by winged males or walks by wingless females. Dwelling within these narrow silk domiciles has apparently constrained their body form, as vividly reflected in the form of females, which are wingless, streamlined, and very flexible (Ross, 2000). Their tarsal silk glands (Mukerji, 1927; Barth, 1954; Alberti and Storch, 1976; Nagashima *et al.*, 1991; Dubitzky and Melzer, 1999) are unique for hexapods (Craig,

¹Department of Biology, Santa Clara University, Santa Clara, California 95053.

²To whom correspondence should be addressed. E-mail: jedgerlyrooks@scu.edu.

1997), although embiidids are not the only insects to use their front feet to manipulate silk [e.g., worker ants (Fisher and Robertson, 1999)].

A recent review of molecular and functional aspects of silk reveals that silk proteins produced by arthropods may have evolved from a common ancestor (Craig, 1997). Despite this antiquity, of the insects that produce silk, only those in three orders (Embiidina, Hymenoptera, and Lepidoptera) have evolved spinning behavior. Spinning refers to actions which pull and shear the silk as it issues forth from glands causing the molecules to orient into sheets (see Craig, 1997). Other producers of silk, for example, psocopterans, secrete, eject, or deposit silk directly on the substrate. Of the insects that spin, only embiidids do so throughout life.

Spinning behavior has been detailed for caterpillars (Fitzgerald *et al.*, 1991), ants (see Fisher and Robertson, 1999), and spiders (see Craig, 1997). Spinning by embiidids has been described but not quantified (e.g., Imms, 1913; Mills, 1932). The present study describes the basic motions of spinning and explores variation within the order by comparing spinning behavior and construction techniques of three species: *Antipaluria urichi* (Saussure) (Clothodidae), *Pararahagadochir trinitatis* (Saussure) (Embiidae), and *Oligotoma saundersii* (Westwood) (Oligotomidae). Adult males were not evaluated because they do not contribute to construction of silk domiciles. Colony composition in relation to the expanse of silk in field colonies was also assessed for *P. trinitatis* and *O. saundersii* for comparison to *A. urichi*, previously studied by Edgerly (1987a,b, 1994, 1997).

Silk covers foraging zones that are extended as individuals seek fresh food (lichens and algae for species in this study) at the edge of the silk and provides a retreat area where they rest and lay eggs. Adult *A. urichi* females spin copious amounts of silk, especially after their eggs hatch (Edgerly, 1988), and this silk offers some protection from predators in their tropical forest habitat (Edgerly, 1994). Ross (2000) has observed embiidids worldwide producing extensive silk patches and/or tube-like galleries on the bark of trees, some even covering entire trunks. Others occupy subterranean galleries spun along crevices in the soil. Despite this variation, Ross noted retreat areas and foraging zones in silk of webspinners throughout the world.

In the present study, focal sampling techniques were employed to document and compare the behavioral repertoires of silk spinning for *A. urichi*, *P. trinitatis*, and *O. saundersii*. In addition, for an evaluation of species-specific construction techniques, adult females of each species were allowed to spin silk on similar substrates for nine days. Spinning actions were analyzed by detailed inspection of videotaped adult females of *A. urichi*. Finally, in the field, the coverage (cm²) of silk was measured and the number of individuals sharing silk was counted to allow determination of colonial tendencies for

P. trinitatis and *O. saundersii* for comparison with previous studies of *A. urichi* (Edgerly, 1987b; 1994).

METHODS

Behavioral Repertoire of Silk Spinning

Time budgets of silk spinning were observed for adult females residing separately on bark pieces in a laboratory in Trinidad ($N = 5$ for *A. urichi*, $N = 5$ for *P. trinitatis*, $N = 10$ for *O. saundersii*). To trigger spinning, each female's silk was removed with forceps, causing her to spin anew. Remnants of silk provided a focal point for the female to begin replacing her silk. At the onset of spinning, her actions were recorded with a laptop computer configured using The Observer (by Noldus). Each female was observed once. Behavioral acts were timed and the entire sequence was recorded. The session ended when a female stopped spinning for 5 min so that the duration of each bout was dictated by the female's activity. The proportion of time engaged in each activity and the frequency of events were compared as a function of species using a one-way analysis of variance conducted with the SAS Institute's statistics program JMP-IN. Proportional data were transformed prior to analysis using the angular transformation.

Choreography of Silk Spinning

A. urichi was selected as a videotape model for an investigation of details of spinning due to its large size [mean length = 1.61 ± 0.015 (SE) cm (Edgerly, 1987a)]. In addition, *Antipaluria* is in the most primitive family in the order [Clothodidae (see Szumik, 1996)] and may express the basic spinning technique of embiids. *A. urichi*, collected in Trinidad, were reared from eggs in the laboratory at Santa Clara University. Adult females were videotaped as they replaced torn silk or patched holes during a 20-min session. Two of three females stayed in clear view of the camera for a total of 14 min 35 s. Only these females were evaluated. The position of the right front tarsus of one female appeared in sharp focus for 5 min 40 s while she spun. The foot's position was sketched in a numbered sequence onto clear acetate sheets placed against the image on the monitor. These positions were translated into a choreographic representation. The second female patched a hole in preexisting silk, rather than creating a new patch. This bout of 67 s was documented in the same manner as described above.

Construction Techniques in Arboreal Embiids

Adult females constructed silk coverings on pieces of sloughed bark that were obtained from a leguminous tree (*Enterolubium cyclocarpum*) on which embiids lived in the field. Each female ($N = 7$ for *A. urichi*, $N = 9$ for *P. trinitatis*, $N = 11$ for *O. saundersii*) was placed on a piece of bark (roughly 9×4 cm) that supported lichens and algae on its surface, thus providing food. Each bark piece was held in a clear plastic beverage cup (15 cm tall) capped with fine mesh. At 24, 48, 96, and 216 h, each female's silk covering was examined and drawn to scale including the extent of silk, the location of the female, and the positions of frass and bitten pieces of bark that were stitched into the silk or placed on its surface. Drawings were rendered in the afternoon when the embiids were resting [feeding occurred at sunset and after dark (unquantified observations)]. Because silk covers relatively flat bark, the silk covering, essentially a two-dimensional structure, was measured as an area. A female's retreat area was defined as the site where she was consistently found at rest during the observation period. Again, proportional data were transformed using the angular transformation before conducting statistical testing.

Silk and Its Occupants in the Field

In August 1998, the relationship between the extent of silk and the number of occupants was determined for field colonies of *P. trinitatis* and *O. saundersii*. The term "colony" refers to occupants sharing silk. All silk that was connected, even by narrow silk galleries, was considered to be one domicile because embiids travel within silk passageways and can interact with any individual sharing that silk. The term "domicile" is used instead of "nest" because embiids do not bring food back to the silk covering from the outside as they would if silk functioned as a nest. Rather, food is enveloped by silk and is depleted over time. The silk domicile, therefore, acts as a covering for food and a retreat site for resting and for guarding eggs. Colonies for this study lived on nonnative trees growing on the campus of the University of West Indies (UWI) in St. Augustine. In addition, *O. saundersii* colonies living on coconut palms along the northeast coast near Toco were also measured.

Sample colonies resided on bark up to 150 cm from ground level on five randomly selected ornamental trees for both species at UWI and on five coconut trees for *O. saundersii* at Toco. The sampling area on each tree supported only one species of webspinner. A grid with guidelines (1×1 cm²), drawn on clear acetate, was placed against the silk and the squares that encompassed silk of one domicile were counted. The distance to the nearest

domicile for all colonies was measured to reflect the colony density in the sampling area.

Additional domiciles ($N = 264$) were destructively sampled and evaluated for silk area as a function of number of occupants, sorted by developmental stage and by sex of adults. An adult female sitting alongside nymphs was categorized as “female with nymphs”; a female resting on top of or next to eggs was designated “female with eggs.” At Toco, all colonies of *O. saundersii* ($N = 156$) up to 150 cm were evaluated. At UWI, 60 colonies of *P. trinitatis* on five trees and 48 colonies of *O. saundersii* on four trees were measured. For both species, the 12 colonies sampled per tree were selected randomly. To do so, each tree was divided into 30° intervals around the trunk, as if the trunk were a 360° circle. At each interval, a colony was selected by drawing a number, ranging from 1 to 11, from a shuffled deck of cards. The number was multiplied by 15; the product was used to indicate how many cm up from the ground we needed to go to find the sample colony.

Analysis of variance and *t* tests were used for all comparisons. Silk expanse (cm^2) was transformed by taking the square root to adjust for non-normality.

RESULTS

Behavioral Repertoire of Silk Spinning: Event Recordings

Observation periods for each species did not differ ($F = 0.98$, $df = 2$, $P = 0.39$): *A. urichi* was observed for, on average, $1,749 \pm 297$ (SE) s; *P. trinitatis* for 1254.9 ± 285 s; and *O. saundersii*, for 1693 ± 210 s. Females in each species expressed a similar style of spinning silk and closely resembled the videotaped *A. urichi* females (see below). First, they spun silk over their backs, creating silk scaffolding that they subsequently reinforced. As they spun, they moved forward and back while adding silk. They also turned 180° at some point and continued spinning. Next, they rotated their bodies to face their venter toward the silk and continued to reinforce the developing silk cover. They often antennated, simultaneously touching the silk with their mouthparts, perhaps checking for gaps. They pushed up against the silk with their heads and their middle legs that extend perpendicular to the long axis of the body.

Behavioral acts exhibited by each species were similar, although the times devoted to each act varied in species-specific ways (Figs. 1 and 2). They devoted approximately the same time to sitting still, walking, antennating, and biting silk (Fig. 2B). *A. urichi* and *P. trinitatis* resembled each other in their tendency to spin silk without incorporating frass and/or gathered materials (Fig. 2A). The ratio of time spent clipping bark, gathering frass, and

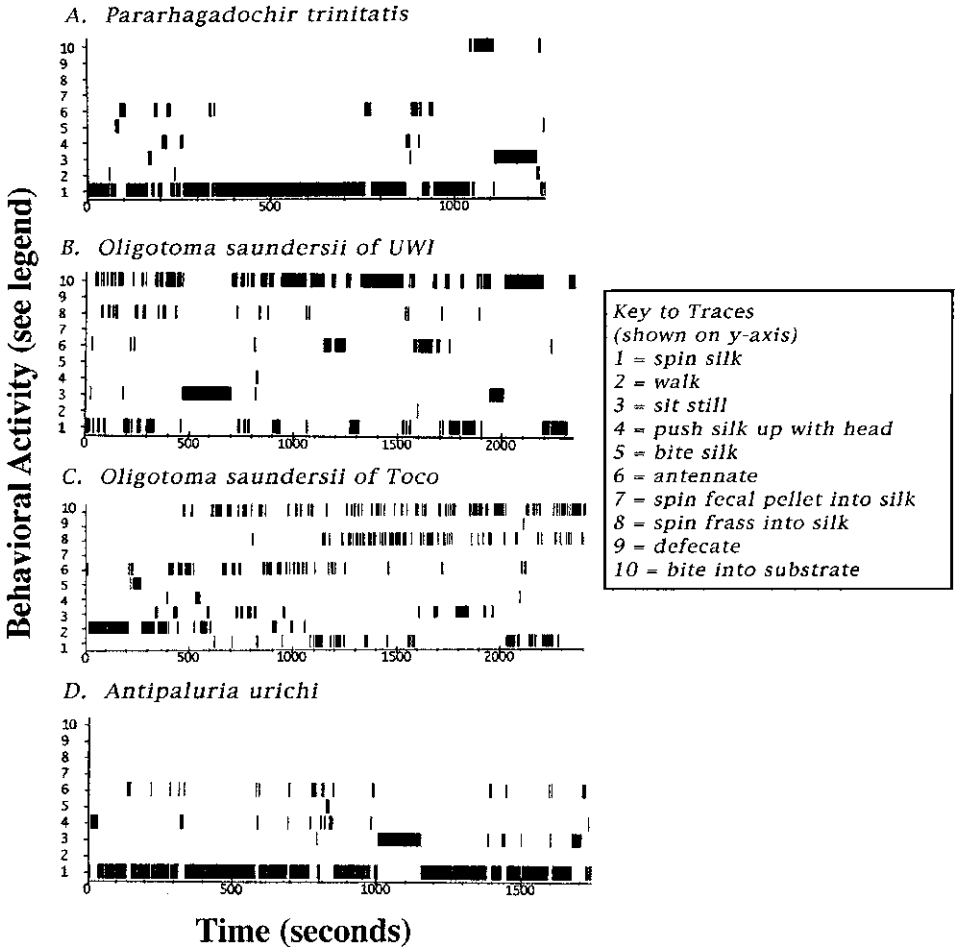


Fig. 1. Behavioral activity during silk spinning as a function of time for females of three species of web-spinners collected in Trinidad. *Oligotoma saundersii*, shown in B and C, is represented by two females from different populations (University of West Indies in B and Toco on the northeast coast in C). The key gives the behaviors, coded as numbers on the y axis. The graph illustrates time series that reflect typical behaviors displayed by females of the different species as they replaced silk that was torn by us in the laboratory. An observation period ended when the female ceased spinning for 5 min. See Fig. 2 for a detailed summary.

silking the pieces into the covering to the time spent spinning was significantly higher for *O. saundersii* [1.49 ± 0.27 (SE)] than for the other two species (0.015 ± 0.015 for *A. urichi* and 0.019 ± 0.014 for *P. trinitatis*; $F = 7.49$, $df = 2$, $P = 0.005$). *O. saundersii* females moved more quickly, switching rapidly from one behavior to another, as reflected in the greater number of events



Fig. 2. Percentage of time spent in each activity during silk replacement sessions for females of each of three species of web-spinners, *Antipaluria urichi* ($N = 5$), *Parahagadochir trinitatis* ($N = 5$), and *Oligotoma saundersii* ($N = 10$). Results of an analysis of variance are shown above the respective means. (A) Activities that differed significantly for the three species. (B) Activities that did not differ significantly for the three species.

on average [0.059 ± 0.0084 (SE) event per s] compared to the other two species (0.034 ± 0.0059 for *A. urichi* and 0.0254 ± 0.0084 for *P. trinitatis*; $F = 6.75$, $df = 2$, $P = 0.007$).

Choreography of Silk Spinning

Videotaped *A. urichi* females alternated between using the left and using the right prothoracic legs to spin. Movements of the right leg for a female creating a new patch of silk are in terms of (1) the number of strokes (for footsteps), (2) the time taken for each cycle of spinning, and (3) the position of the leg during a cycle. With each stroke, the female lifts her leg and then touches the substrate, preexisting silk, or her dorsum, while many strands of silk are released from numerous silk ejectors on the tarsus. A cycle is defined as all strokes during a spinning bout starting at the anteriormost position, continuing with all strokes taken to the side and over the dorsum, until the leg is returned to the anteriormost position. One can envision a cycle of strokes by imagining the embiid in the center of a clockface with her head at 12:00 and her cerci at 6:00. Her right tarsus might touch the numbers in the following order: 2, 4, 5, 6, 7, 8, 9, 4, 2, 1 (this example is based on 1 of the 20 cycles recorded from the videotape). A summary of one cycle of the right leg is shown in Fig. 3.

Spinning cycles ($N = 20$) averaged 4.8 ± 0.78 (SD) s, with 1.85 ± 0.24 strokes per s and 8.9 ± 1.92 strokes per cycle. Various positions displayed during videotaping are shown in Fig. 4. After ending a cycle, the videotaped female either repeated a cycle on the right, spun with the left leg, or engaged in another activity such as antennating, sitting, or moving. The first silk strands appeared to be attached to the setae on her dorsum and subsequently all were attached to existing silk. The developing band of silk across the back can be seen as a thickened strand crossing the back of the female in Fig. 4.

A videotape recording showed another female with her ventral side facing a hole that she was patching. She attached silk to preexisting silk on the sides of the hole, drawing her foot across the hole and attaching silk to the opposite side. The routine resulted in the formation of a patch (Fig. 5). The videotaped females also reinforced their silk structures for 4.6 min during the 20-min session. To do so, a female faced her venter against the developing silk patch and rapidly punched her front tarsi against the silk, near the ventral surface of her head. The motion resembles kneading bread. The females repeatedly alternated from the right to the left leg as they added silk strands to the framework of silk originally produced by the spinning cycles described above.

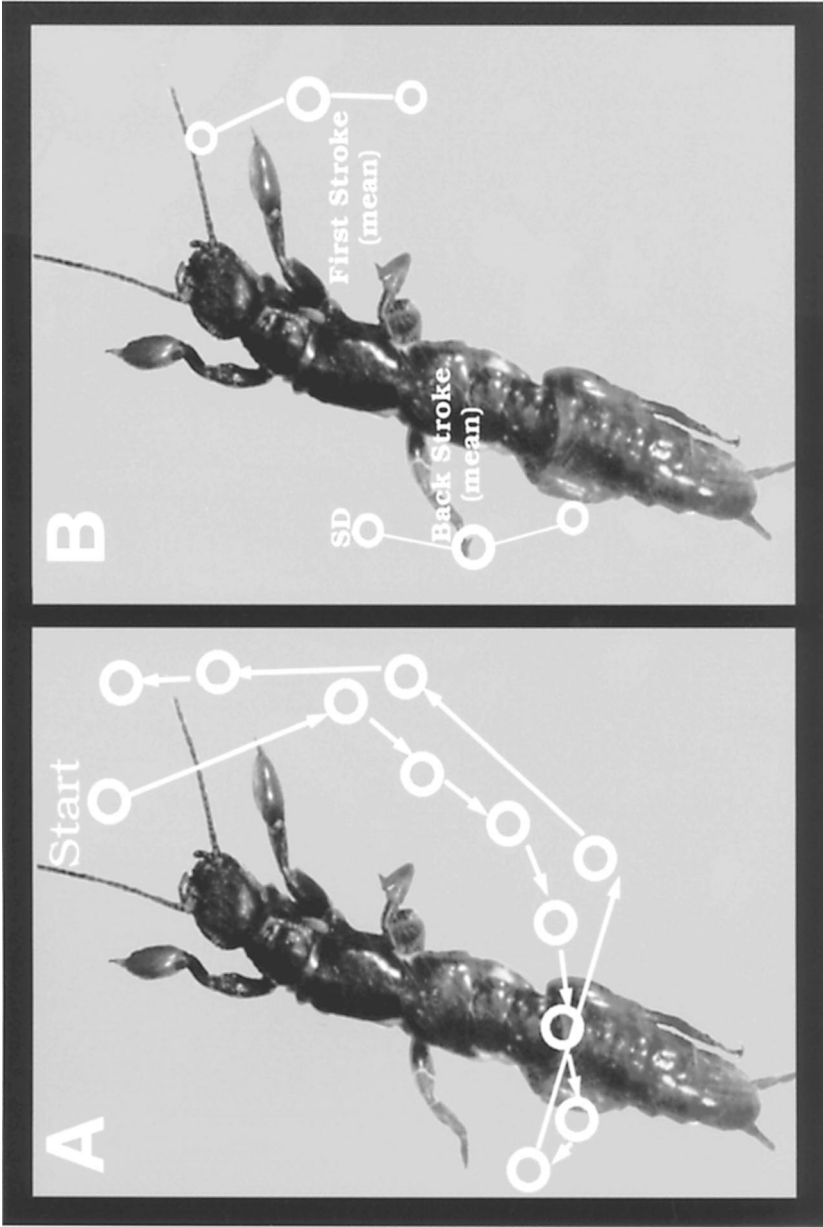


Fig. 3. A cycle of spinning by *Antipaluria urichi* producing a silk covering. The summary is based on analysis of video replayed in slow motion. The white graphics are superimposed on a photographic image of an adult female. Each white circle indicates a point when the female touches her foot to preexisting silk and the arrows show the direction in which she swung her foot after each touch. Silk is attached to the substrate when the foot touches it. (A) Analysis of one cycle of spinning to the right side. (B) The average positions of the first and last strokes for 20 cycles of spinning. The average positions are indicated by the larger white circles; the range is 1 standard deviation above and below the mean as indicated by the smaller white circles.

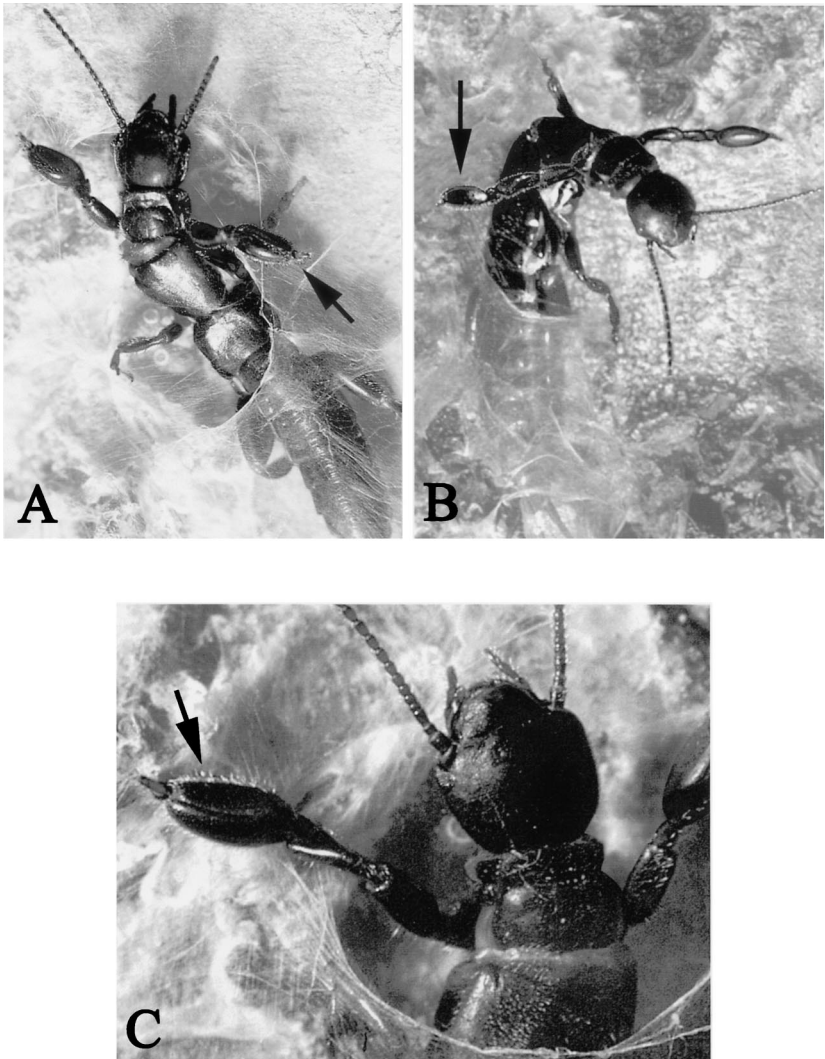


Fig. 4. Photographs of *Antipaluria urichi* females spinning silk. (A) Sidestroke to the right. (B) The backstroke (over the dorsum). The front tarsus involved in spinning is indicated by a black arrow in each case. (C) Silk ejectors are visible as white hair-like structures on the ventral side of the left front tarsus, indicated by the arrow.

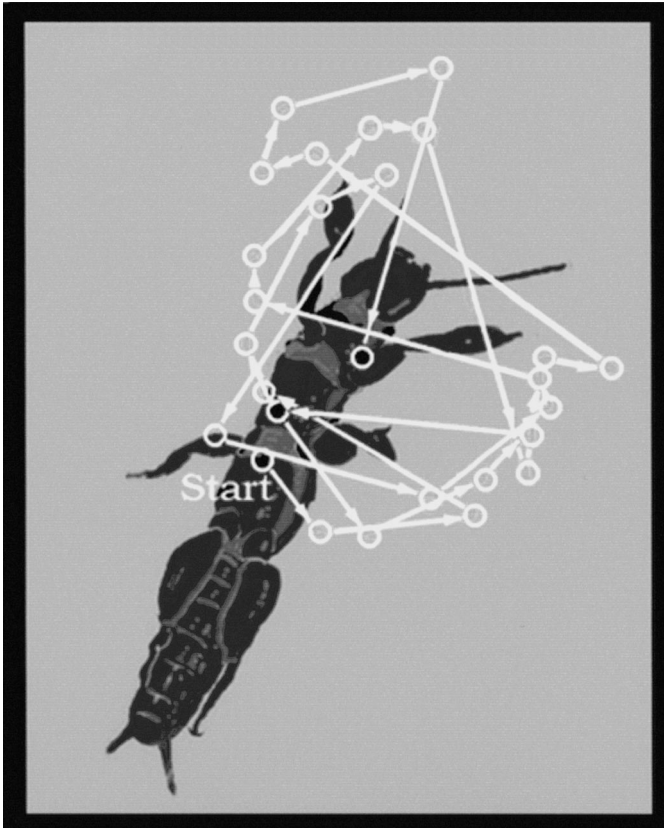


Fig. 5. Summary of the spinning cycle of an *Antipaluria urichi* female patching a hole. Her body is shown ventral side up and is drawn based on slow-motion video images. The white circles represent positions of her right front foot. The female touched her front tarsus, multiple times, to the sides of the hole that was torn in her silk covering, then she pulled the silk across the hole which is directly above her body.

Construction of a Silk Domicile in the Laboratory

Silk coverings produced over 216 h in the laboratory typically had three sections: a retreat, an outer covering that resulted as the embiids extended their foraging zone, and silk galleries. Tube-like galleries developed as a female reinforced the silk around her body while traveling back and forth between the retreat to new foraging sites.

In the laboratory, an opaque, silk retreat area was obvious in *P. trinitatis* and *A. urichi* as distinct from the more transparent foraging zone. Of

the three species, *P. trinitatis* had the smallest retreat relative to its overall silk area ($F = 76.5844$, $df = 2$, $P < 0.0001$) (Fig. 6), although the total silk area produced during the 216 h for females of the three species was not significantly different ($F = 3.1147$, $df = 2$, $P = 0.0627$). All females used frass and/or gathered materials in construction, but the extent of the refuse coating varied between species (Fig. 6B) ($F = 96.9714$, $df = 2$, $P < 0.0001$). Females incorporated frass into the silk along the sides or in the top layer, a behavior that may function to clear pathways. *O. saundersii* females differed from the other two species in that they clipped, gathered, and then scattered materials over all sections of their retreat and foraging zone. The retreat area for this species had thick silk with a very dense coating of refuse.

Characteristics of Silk in the Field

Silk persists even when a site is abandoned, and as such silk remnants give clues about dispersal and colonization attempts in a population. In the field, silk coverings were variably intact or tattered, and varied from occupied to abandoned. As in the laboratory, domiciles often included thickly reinforced retreats and thinner foraging zones. For example, the silk of *P. trinitatis* included narrow galleries, which built up under broader outer coverings (Fig. 7A). *P. trinitatis* silk stood out from the background as a shiny patch, colored white and tinted with lavender. For *O. saundersii*, silk galleries followed bark crevices when available and were generally covered with frass and pieces of substrate (Figs. 7B and C).

The circumference measured at breast height of trees at UWI supporting *O. saundersii* colonies averaged 4.14 ± 0.032 m, whereas the coconut trees at Toco colonized by this species averaged 0.72 ± 0.011 m. The silk expanses of *O. saundersii* reflected this difference in that UWI silk domiciles were significantly larger on average [8.39 ± 0.798 (SE) cm^2 ; $N = 512$] than those found at Toco (3.79 ± 0.456 cm^2 ; $N = 154$; $t = 3.122$, $df = 664$, $P = 0.002$). For the latter population, silk of 154 of 156 colonies was analyzed because two colonies were mostly hidden within crevices and could not be accurately measured. Within each *O. saundersii* population, the square root of the silk expanse was not related to the tree circumference (for UWI, $F = 0.467$, $df = 1$, $P = 0.49$; for Toco, $F = 0.013$, $df = 1$, $P = 0.91$). *P. trinitatis* silk (23.19 ± 0.235 cm^2 ; $N = 622$) measured at UWI also did not vary in size as a function of tree girth on average 5.42 ± 0.096 (SE) m ($F = 0.849$, $df = 1$, $P = 0.357$). Silk of *P. trinitatis* was significantly more expansive than that of *O. saundersii* in either population ($F_{2, 1288} = 79.405$, $P < 0.0001$). This difference in silk expanse was not a reflection of female size,

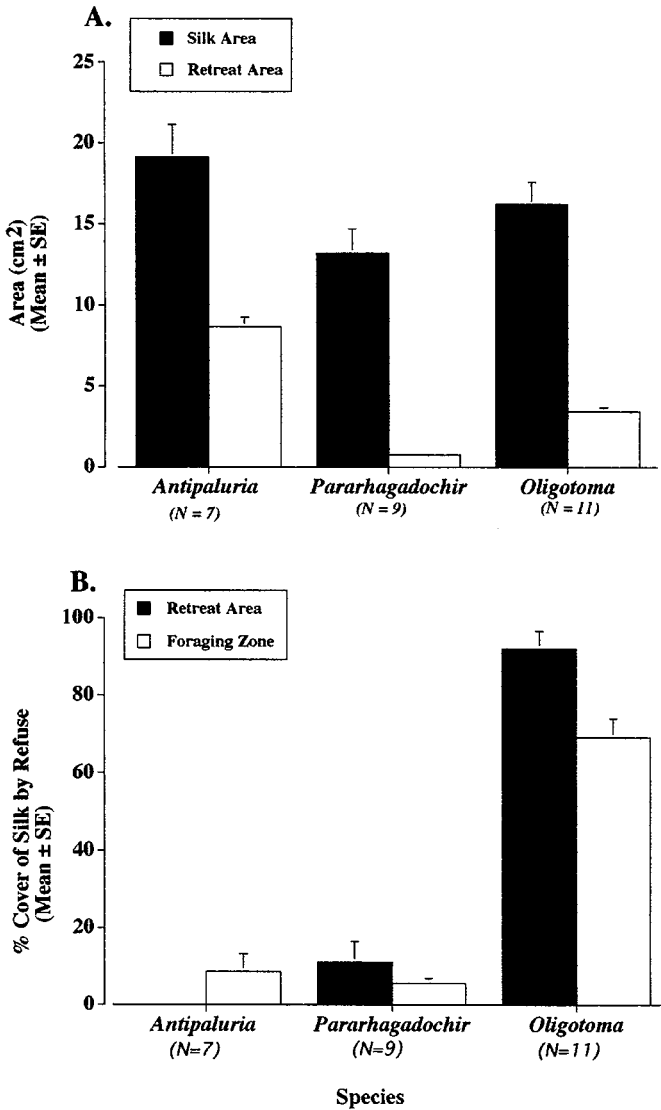


Fig. 6. Area of silk spun by females of three species of webspinners (*Parahagadochir trinitatis*, *Oligotoma saundersii*, and *Antipaluria urichi*) placed on bark pieces in the laboratory in Trinidad. Silk was produced over 216 hours. (A) Mean area of silk and extent of the retreat that is distinct in opacity and quantity of refuse (including frass and gathered substrate materials). The retreat is where the female spends her time resting during the day. (B) Percentage cover by refuse spun onto the retreat area and foraging zones.

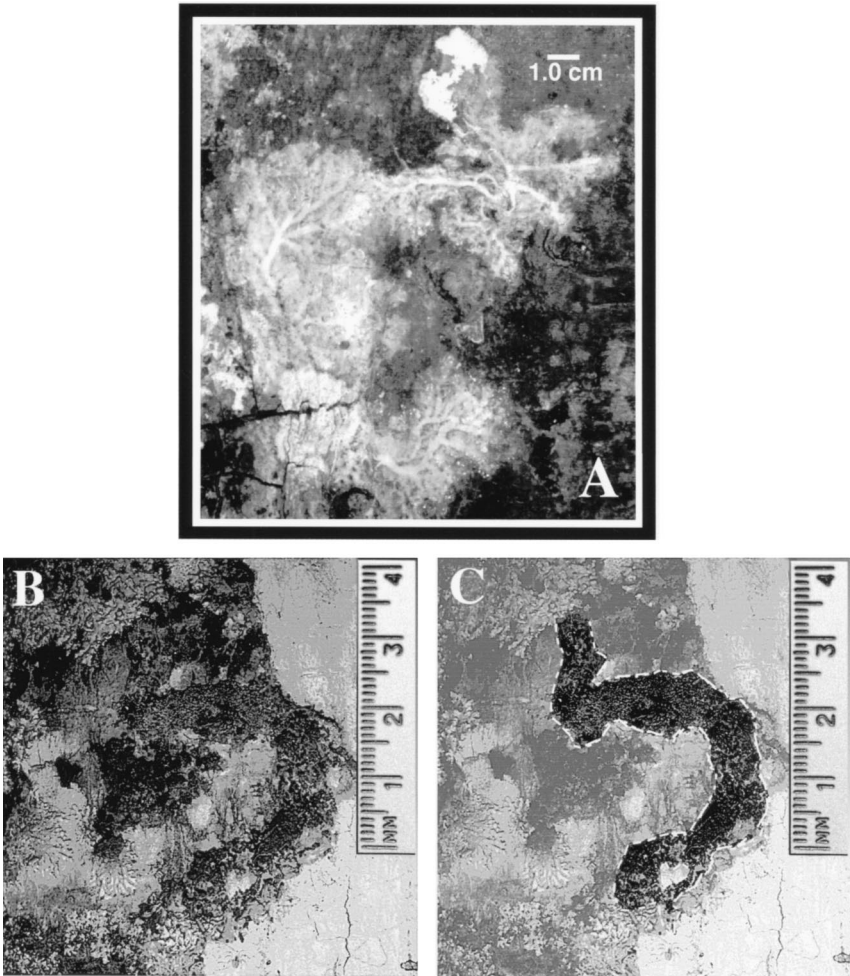


Fig. 7. (A) Field colony of *Pararhagadochir trinitatis* on tree bark. The white patch at the top center is lichen, partially consumed by the eriophagids. Tube-like silk galleries are visible through the outer thin layer of silk; these are pathways that build up over time as the webspinners travel from their daytime retreats to the edges of the silk covering where they feed. The silk of this species is shiny and sparkles under normal sunlight; this feature is visible as tiny spots of white on the silk in the photograph. (B) Field colony of *Oligotoma saundersii* in natural lighting; (C) with the contrast altered digitally to reveal the camouflaged dwelling place constructed of silk, frass, and bark chips.

however, as *O. saundersii* females ($N = 21$) from the Toco population lived in smaller domiciles but were significantly longer in body length [$F_{2,45} = 6.114$, $P = 0.005$; mean length = 0.91 ± 0.02 (SE) cm] than females of either species from UWI [*P. trinitatis*, 0.80 ± 0.027 cm ($N = 12$); *O. saundersii* at UWI, 0.82 ± 0.02 cm ($N = 21$)]. Nearest-neighbor distances from one silk covering to the next did not vary significantly for the three populations [*P. trinitatis*, mean = 4.9 ± 4.5 (SD) cm; *O. saundersii* at UWI, mean = 5.6 ± 12.36 cm; *O. saundersii* at Toco, mean = 4.9 ± 3.2 cm; $F_{2,1202} = 1.0263$, $P = 0.36$].

Colony Composition

Generally, the more individuals comprising a colony, the greater the silk expanse (Fig. 8). For both species, the silk expanse was significantly greater for currently occupied versus abandoned domiciles (Fig. 9). The number of individuals per colony in occupied silk domiciles was significantly higher on average ($F = 4.138$, $df = 1$, $P = 0.04$) for *P. trinitatis* [mean = 6.31 ± 0.908 (SE); $N = 41$] than for *O. saundersii* at both locations (mean = 3.22 ± 0.85 ; $N = 113$). The average number of *O. saundersii* individuals per colony at UWI (mean = 4.70 ± 2.63 ; $N = 27$) was intermediate between that of *P. trinitatis* and that of the population at Toco (mean = 2.76 ± 0.767 ; $N = 86$). *O. saundersii* colonies at UWI were also more variable than those at Toco.

Residents sharing silk included adult females alone, females with eggs and/or nymphs, and nymphs alone (Fig. 10). Only five adult males were discovered in the sample. Numerous silk coverings, from 32 to 42% of the total measured per population, were empty. The tendency for females to share silk with other adult females varied; none of the 21 adult females in the Toco population shared silk with another adult, whereas 7 of the 27 *P. trinitatis* females and 15 of the 26 UWI *O. saundersii* females lived in colonies (Fig. 10). In one of those colonies, only 2 of 10 females tended eggs; the other 8 resided with nymphs ($N = 62$). Another colony housed five females (one with eggs, one with newly hatched nymphs, and three apparently nonreproductive). Nymphs were found either with adult females or by themselves (designated "alone" in Fig. 10). Nymphs with adult females were in larger groups than those without (Fig. 11) ($F = 15.69$, $df = 1$, $P = 0.0001$). This difference was not related to species ($F = 0.479$, $df = 1$, $P = 0.49$), nor did a significant interaction between species and living situation for the nymphs appear ($F = 0.6612$, $df = 1$, $P = 0.4182$). Only *O. saundersii* from Toco ($N = 68$ colonies) were used in this comparison with *P. trinitatis* ($N = 41$ colonies) because only 3 *O. saundersii* colonies of the 48 sampled at UWI had nymphs and females together, and therefore that sample is too small to allow statistical testing.

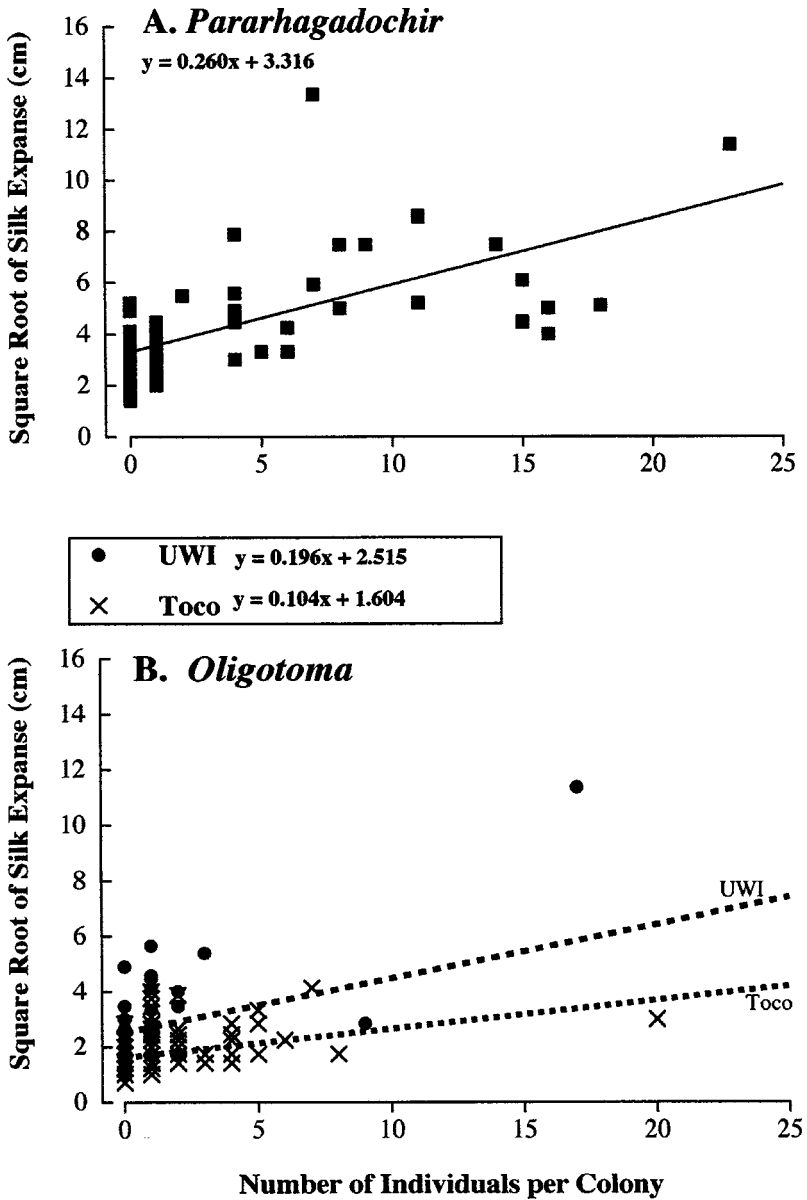


Fig. 8. Square root of silk expanse (cm) as a function of the number of individuals occupying each silk gallery. Many points represent more than one observation. The best-fit lines and associated linear equation are shown to clarify the relationship. We omitted two outliers (one at $N = 64$ individuals for Toco and one at $N = 71$ for UWI). The R^2 values did not change with or without these points. (A) For *Pararhagochir trinitatis* colonies, the expanse of silk was significantly related to the number of individuals ($F = 37.2$, $N = 60$, $P < 0.0001$; $R^2 = 0.39$). (B) For *Oligotoma saundersii* colonies in each of two populations, UWI and Toco, the relationship was also significant (UWI— $F = 102.886$, $N = 48$, $P < 0.0001$; $R^2 = 0.69$; Toco— $F = 141.39$, $N = 154$, $P < 0.0001$; $R^2 = 0.48$).

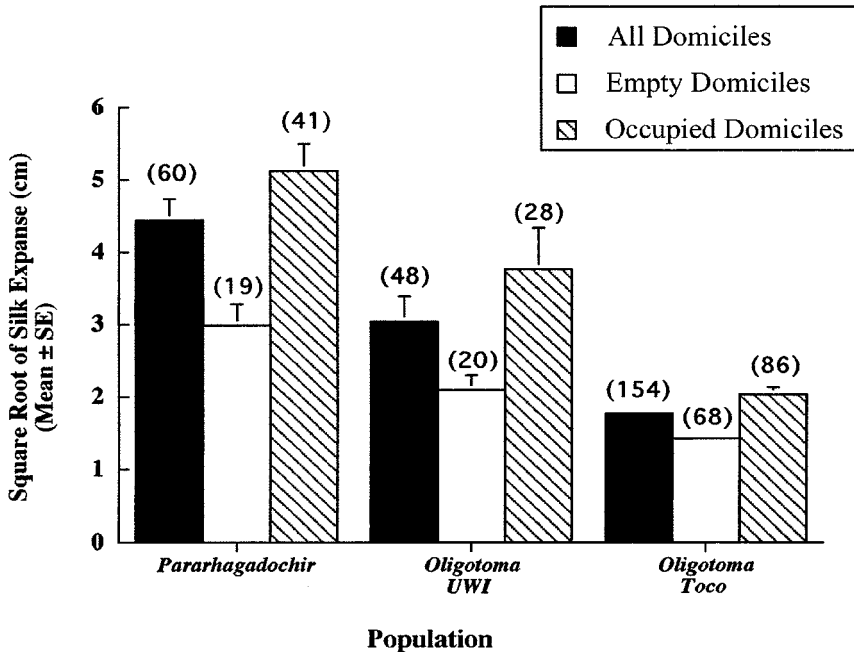


Fig. 9. Comparison of silk expanse for occupied and empty silk domiciles for three populations of embiids. The number in parentheses above each bar represents the number of colonies in each category. Occupied silk patches were significantly larger than empty silk (*Pararhagadochir trinitatis*, $t = 3.59$, $P < 0.0007$; UWI *Oligotoma saundersii*, $t = 2.465$, $P < 0.02$; Toco *O. saundersii*, $t = 4.906$, $P < 0.0001$).

DISCUSSION

Comparison of Silk-Spinning Behavior for Three Species of Embiids

Analysis of time budget recordings suggested that spinning by females is similar in these three species. Only *A. urichi* was evaluated using close-up video, but based on observations made during focal sampling, no indication emerged that the other two species varied substantially from the basic spinning technique employed by *A. urichi*. For these species, two routines typified construction of silk scaffolding: (1) spinning in repeated cycles to the front, to the side, and over the back, alternating between the left and the right foot in irregular cycles, and (2) mending small holes by attaching silk to the sides of the hole and then stretching silk across the hole while facing the hole. They also reinforced the silk in similar ways by rapidly punching their front feet against the scaffolding, adding many threads in a short period of time.

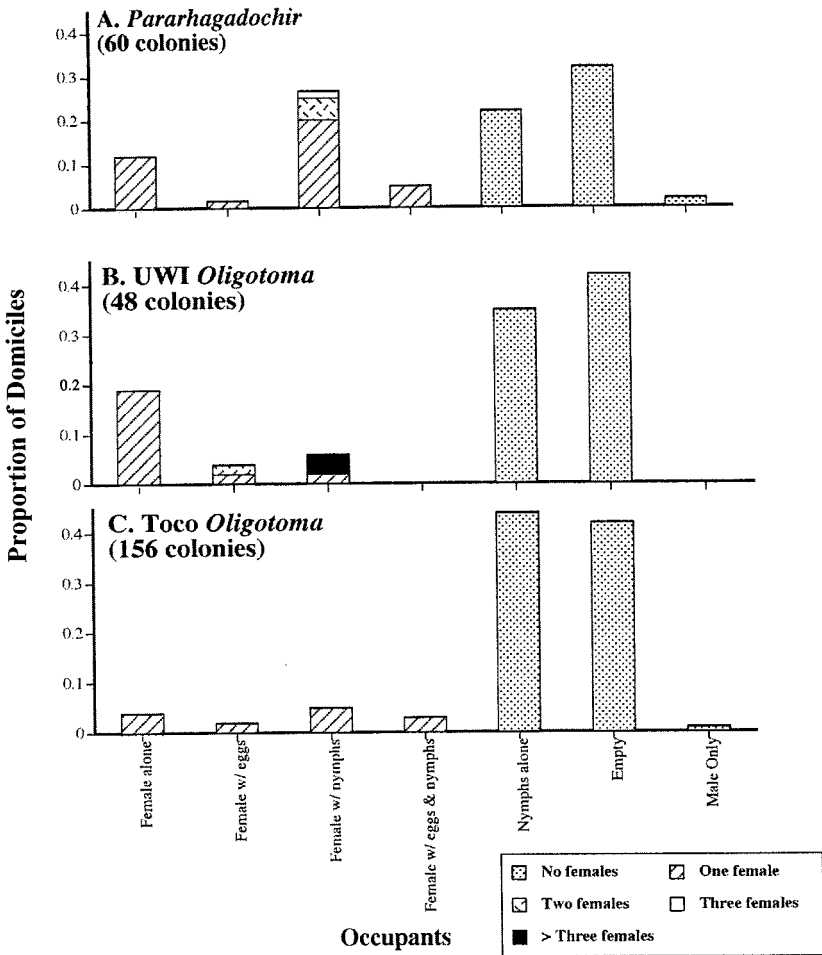


Fig. 10. Proportion of domiciles containing different stages in the life cycle for *Pararhagadochir trinitatis* (A) and *Oligotoma saundersii* (B and C, two populations) in Trinidad.

When allowed to spin for many days in the laboratory, embiids also incorporated materials into the silk to a greater or lesser extent, depending on the species. Construction techniques, therefore, involve attaching silk to a substrate that becomes part of the dwelling place, as silk-spinning caterpillars are known to do (Fitzgerald and Willer, 1983; Fitzgerald *et al.*, 1991). In one detailed investigation of the use of silk, Fitzgerald *et al.* (1991) determined that caterpillars generate forces by stretching silk that then retracts to facilitate the tying, rolling, or folding of leaves of the host plant. Unlike

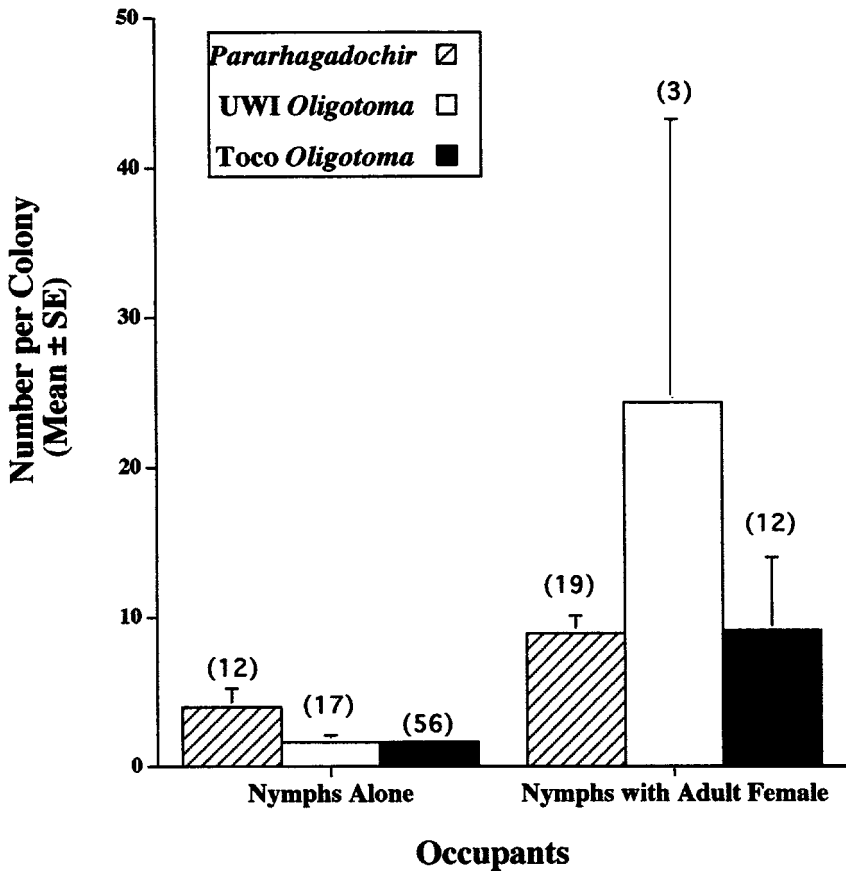


Fig. 11. The mean number of nymphs found in colonies either alone or with adult females for two species of web-spinners: *Pararhagadochir trinitatis* at UWI and *Oligotoma saundersii* at UWI and at Toco. The number in parentheses above each bar shows the number of colonies containing nymphs in each category.

caterpillars, embiids use their numerous silk ejectors to produce multiple strands of silk at one time. Their complex silk structure does not appear to contract or change after it is spun. We also found that embiids produce substructures within their dwellings by attaching new silk to preexisting silk. These substructures, tubular passages visible through an upper layer of silk, become reinforced with frass over time. The contribution of and/or interaction among possible forces generated by changes in newly secreted silk, spinning behavior, and reinforcing of silk with other materials remains to be investigated.

The incorporation of extraneous materials and frass into the silk was shared by the three species, but the intensity of this behavior was exaggerated in *O. saundersii*. Field domiciles reflect this difference, as silk of *A. urichi* is sparkling white, silk of *P. trinitatis* is shiny lavender–white, and silk of *O. saundersii* is virtually undetectable and camouflaged, at least in the Trinidad population of this widely distributed, exotic species. Adding bark chips to silk appears in another silk-spinning insect, *Melisotarsus emeryi* (Fisher and Robertson, 1999). Worker ants of this species integrate wood fragments into their silk when sealing exit holes. The spinning behavior of these ants shows a remarkable resemblance to that of embiids because they use their front feet to spin. Silk is secreted by hypostomal silk glands but they pull the silk out with specialized structures on their front feet. They then apply silk strands, with their feet, to the hole and to a wood particle used to seal the hole. The ant’s spinning behavior, described by Fisher and Robertson as “kneading,” surely resembles the two-step “punching” behavior displayed by embiids. In both cases, such motions yield numerous strands of silk that are quickly incorporated into a patch.

Many interesting questions about spinning by embiids remain to be addressed. For example, the flexibility of embiids to respond to different substrates and to different types of damage in their silk remains unknown. The apparent gathering of sensory information by their antennae, mouthparts, and cerci during spinning is intriguing as well. Pushing up with the body against the silk during spinning also suggests that some information may be gathered by receptors in their leg joints, unless they are merely stretching the silk. Behavior in subterranean webspinners also has not been described, to our knowledge. Observations of populations of *O. saundersii* living under rocks, as in China (Ling, 1935), might reveal whether they apply the same style of silk preparation that they do when on bark. In addition, developmental and sexual differences have not been explored. Adult males have been seen spinning silk around females during courtship. Such silk may temporarily shield females from other males that try to court them or try to interfere with mating pairs (Edgerly personal observation). In *Anisembia texana* (Mel.) (Anisembiidae) when other embiids try to enter their retreat areas, resident females seem to produce a defensive silk, of a quality different from that of the silk covering (Choe, 1994). The functional attributes of silk also remain unresolved, despite the suggestions in the literature of their antipredator and protective functions (Edgerly, 1994; Ross, 2000).

Sharing Silk: Colony Composition in the Field

Based on the distribution and composition of colonies of *O. saundersii* and *P. trinitatis*, we conclude that females, as either nymphs or adults, disperse

prior to oviposition, spin a small patch of silk, and prepare and tend their egg masses. This interpretation is based on the observation that females, alone or with eggs, occupy small patches of silk. The study populations also appeared to be densely packed as reflected in the short distances, approximately 5 cm between patches of silk.

After their eggs hatch, females stay with their nymphs, at least for a while. The high proportion of nymphs living without adults and within small patches of silk suggests that nymphs leave their mothers at some point prior to reaching adulthood. The smaller expanse of nymphal silk indicates that some offspring leave the more expansive silk walls spun by their mothers. Studies of nymphal development in other embiid species have demonstrated that, in the presence of their mothers, nymphs perform better for a variety of reasons (Edgerly, 1988; Rita, 1992; Choe, 1994). For *A. urichi*, which are similar in their arboreal habits to the current subjects, females create much of the silk covering for their nymphs, especially while they feed at the periphery of the colony (Edgerly, 1988). This act alone may contribute to higher nymphal survival and may partly explain why, in the present study, the nymphs with adult females are found in larger groups. Why nymphs would leave maternal silk is not known.

Adult males were uncommon, suggesting that their lifestyle resembles that seen in other species in the order; they emerge as nonfeeding, winged adults that die soon after mating (Ross, 1970).

At UWI, for *P. trinitatis* and *O. saundersii*, sharing of silk by adult females varied from 26% (of 27 females) for the former to 57% (of 26 females) for the latter. The absence of colonial females at Toco, and the presence of some at UWI, suggests that colonies can build up if conditions are appropriate. The difference might be due to the resource availability at our study sites because trees with narrow trunks (coconut trees) supported smaller colonies. In addition, the bark of the coconut trees had large gashes that may have affected the ability of colonies to develop into larger cohesive units. Ling (1935) also found variability in colony sizes for populations of *O. saundersii* in China, depending on the substrate; colonies living under rocks were larger and more complex than those found on trees in the same habitat. This contrasts with a report on another species in the genus; adult *O. humbertiana* (Saussure) of India were never found in colonies (Ananthasubramanian, 1957). The relative abundance of colonial females at UWI resembles that reported for *Embia major* (Imms, 1913). Imms censused 130 colonies under rocks and found that 73 of the 149 females (48%) were solitary. The remainder ranged from groups of two to groups of eight adult females.

Compared to *A. urichi*, *P. trinitatis* and *O. saundersii* had, on average, smaller silk coverings and fewer residents within them. *A. urichi* is a large

webspinner, a feature that correlates well with the extensive silk coverings that they spin. The silk of *A. urichi* colonies is often greater than 1000 cm² in area, sometimes covering entire tree trunks and major limbs, and even reaches 37,000 cm² in one case (Edgerly, 1987b). Furthermore, their colonies vary more in numbers of individuals than found for either species in the current study. For example, one *A. urichi* colony contained 72 individuals, 24 of which were adult females sharing the same silk covering. Of 138 adult *A. urichi* females in 44 colonies, 86% shared their silk with other females at one area in the northern Trinidad. At another site, of 57 females, 37% were colonial. These statistics indicate that *A. urichi* tends toward coloniality. Based on the present study, *P. trinitatis* and *O. saundersii* can also be categorized as facultatively colonial, where adult females show a variable tendency to share silk.

In conclusion, we present this study as a contribution to the larger goal of understanding embiid behavior. Based on laboratory and field observations, we documented details of silk-spinning behavior of three species and detected two construction techniques for embiids living on trees: (1) sheets of silk that cover domiciles and interior tubular galleries that are reinforced over time as the embiids travel between their resting positions and fresh feeding sites at the periphery, and (2) the same configuration but topped with a coating of frass and gathered and/or prepared materials such as bark chips. We also censused *P. trinitatis* and *O. saundersii* in the field to determine how they construct and share silk and how their colonies might compare with *A. urichi*, whose populations in Trinidad were investigated in previous studies. Our conclusion is that all three species reside in mother-offspring associations and sometimes form colonies with more than one adult female.

Puzzles emerge from the present survey, one being the preponderance of empty patches of silk in the field. This might reflect high failure rates for emigrants or might result from an antipredator response that we detected during our census of *O. saundersii*. Disturbance of their silk caused individuals to bolt and drop to the ground. *P. trinitatis* and *A. urichi* more typically retreated into bark crevices or remained under remnants of silk. These species-specific differences in their reactions to forceps may mimic their reactions to potential predators. Differences in antipredator responses were also noted during recent surveys of embiids in Australia (Edgerly, personal observation). One species of *Notoligotoma* (Notoligotomidae) lives exposed on granite boulders in silk galleries. When their silk was disturbed, the embiids bolted as *O. saundersii* did. Another species in the genus *Australembia* (Australembiidae) lives in tightly woven silken tubes within leaf litter on the ground. When disturbed with forceps, they remained still, even to the extent of appearing to be dead when pulled out, touched, and held. Such

different responses to predators may generate some of the differences detected in dispersion of colonies in a population. This idea remains to be tested.

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REFERENCES

- Alberti, V. G., and Storch, V. (1976). Transmissions- und rasterelektronenmikroskopische Untersuchung der Spinndrüsen von Embien (Embioptera, Insecta). *Zool. Anz.* **197**: 179–186.
- Ananthasubramanian, K. S. (1957). Biology of *Oligotoma humberiana* (Saussure) (Oligotomidae, Embioptera). *Indian J. Entomol.* **18**: 226–232.
- Barth, R. (1954). Untersuchungen an den Tarsaldrüsen von *Embolynta batesi* MacLachlan, 1877 (Embioidea). *Zool. Jahrb. (Anat.)* **74**: 172–188.
- Choe, J. C. (1994). Communal nesting and subsociality in a webspinner, *Anisembia texana* (Insecta: Embiidina: Anisembiidae). *Anim. Behav.* **47**: 971–973.
- Craig, C. L. (1997). Evolution of arthropod silks. *Annu. Rev. Entomol.* **42**: 231–267.
- Dubitzky, A., and Melzer, R. R. (1999). Untersuchung des Spinnvorgangs bei *Haploembia solieri* (Ramburi) im REM. *NachrBl. Bayer. Ent.* **48**: 97–103.
- Edgerly, J. S. (1987a). Maternal behaviour of a webspinner (Order Embiidina). *Ecol. Entomol.* **12**: 1–11.
- Edgerly, J. S. (1987b). Colony composition and some costs and benefits of facultatively communal behavior in a Trinidadian webspinner (Embiidina: Clothodidae). *Ann. Entomol. Soc. Am.* **80**: 29–34.
- Edgerly, J. S. (1988). Maternal behaviour of a webspinner (Order Embiidina): Mother–nymph associations. *Ecol. Entomol.* **13**: 263–272.
- Edgerly, J. S. (1994). Is group living an antipredator defense in a facultatively communal webspinner (Embiidina: Clothodidae)? *J. Insect Behav.* **7**: 135–147.
- Edgerly, J. S. (1997). Life beneath silk walls: A review of the primitively social Embiidina. In Choe, J. C., and Crespi, B. J. (eds.), *The Evolution of Social Behavior in Insects and Arachnids*, Cambridge University Press, Cambridge, pp. 14–25.
- Fisher, B. L., and Robertson, H. G. (1999). Silk production by adult workers of the ant *Melissotarsus emeryi* (Hymenoptera, Formicidae) in South African fynbos. *Insectes Soc.* **46**: 78–83.
- Fitzgerald, T. D., and Willer, D. E. (1983). Tent building behavior of the eastern tent caterpillar *Malacosoma americanum* (Lepidoptera: Lasiocampidae). *J. Kans. Entomol. Soc.* **56**: 20–31.

- Fitzgerald, T. D., Clark, K. L., Vanderpool, R., and Phillips, C. (1991). Leaf shelter-building caterpillars harness forces generated by axial retraction of stretched and wetted silk. *J. Insect Behav.* **4**: 21–32.
- Imms, A. D. (1913). Contributions to a knowledge of the structure and biology of some Indian insects. II. On *Embia major*, sp. nov., from the Himalayas. *Trans. Linn. Soc. Lond.* **2**: 167–195.
- Ling, S.-W. (1935). Further notes on the biology and morphology of *Oligotoma saundersii* Westwood. *Pek. Nat. Hist. Bull.* **9**: 261–272.
- Mills, H. B. (1932). The life history and thoracic development of *Oligotoma texana* (Mel.) (Embiidina). *Ann. Entomol. Soc. Am.* **25**: 648–652.
- Mukerji, M. Sc. (1927). On the morphology and bionomics of *Embia minor*, sp. nov. with special references to its spinning organ. A contribution to our knowledge of the Indian Embioptera. *Rec. Ind. Mus.* **29**: 253–282.
- Nagashima, T., Niwa, N., Okajima, S., and Nanaka, T. (1991). Ultrastructure of silk gland of webspinners, *Oligotoma japonica* (Insecta, Embioptera). *Cytologia* **56**: 679–685.
- Rita, C. (1993). Maternal behaviour in a web spinner *Pseudembia flava* Ross (Embioptera: Insecta). *J. Bombay Nat. Hist. Soc.* **90**: 300–301.
- Ross, E. S. (1970). Biosystematics of the Embioptera. *Annu. Rev. Entomol.* **15**: 157–172.
- Ross, E. S. (2000). Embia: Contributions to the biosystematics of the insect order Embiidina. Part 1: Origin, relationships and integumental anatomy of the insect order Embiidina. Part 2: A review of the biology of Embiidina. *Occas. Papers Calif. Acad. Sci.* **149**: 1–36.
- Szumik, C. A. (1996). The higher classification of the Order Embioptera: A cladistic analysis. *Cladistics* **12**: 41–64.