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Life Beneath Silk Walls: A Review of the Primitively Social Embiidina

Janice Edgerly-Rooks

Santa Clara University, jedgerlyrooks@scu.edu

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2 · Life beneath silk walls: a review of the primitively social Embiidina

JANICE S. EDGERLY

ABSTRACT

I review and summarize the scattered information on embiids (Order Embiidina), with an emphasis on details of colony structure and maternal care. I summarize experimental and observational field results from a detailed study on parental and communal behavior of *Antipaluria urichi*, a Trinidadian webspinner. Topics discussed include the function of maternal behavior, interactions with egg parasitoids, antipredator attributes of communal living, and possible functions of silk. I also compare features of webspinner sociality to other communal insects and spiders. In addition, I discuss promising topics for future study, including male dimorphism, the possibility of higher sociality, and communication systems.

INTRODUCTION

Webspinners (Order Embiidina or Embioptera) construct a nest-like structure, exhibit parental care, and commonly live in the tropics where overlapping generations may occur. These attributes represent factors that allow for the evolution of complex social interactions in insects (Evans 1977; Eickwort 1981), making embiids an intriguing order with many research questions yet to be addressed. This cosmopolitan order, including 850 mostly tropical species in 14 families (E. S. Ross, personal communication), has been classified within the Orthopteroidea, which includes earwigs, cockroaches, walkingsticks, mantids, katydids, crickets, grasshoppers and termites (Hennig 1981). In a more recent phylogenetic treatment of hexapod orders (Minet and Bourgoin 1986), Embiidina and Zoraptera are sister-groups within the Polyneoptera, which includes all the orders mentioned above, plus Plecoptera. Boudreaux (1979) also proposed a close phylogenetic relationship between Plecoptera and Embiidina. Confined to warmer regions, webspinners are found only as far north as southern Virginia in the United States; the highest known altitudinal record is 3500 m, in the cloud forests of Cuenca,

Ecuador (Ross, personal communication). Based on extensive collecting throughout the world, Ross (1970) categorized embiids as subsocial (following Michener's (1969) terminology), exhibiting care of eggs and sometimes of nymphs. The term communal, traditionally used to designate social organization in Hymenoptera (*sensu* Wilson 1971), also seems appropriate for those embiids who share a nest-like structure wherein each female oviposits and tends her own offspring.

In this chapter, I summarize information from the scant literature on webspinner behavior and describe attributes relating to group-living and parental care. Despite the anecdotal nature of most reports, the available information provides an intriguing composite of behavior of these relatively rare and generally inconspicuous insects. After a brief literature review, I will summarize my work on social behavior in *Antipaluria urichi* (Clothodidae).

GENERAL REVIEW OF EMBIID BEHAVIOR

Living within silk

The common name, webspinners, refers to the order-wide characteristic of silk-spinning behavior. Nymphs, adult females (which are always wingless) and adult males spin silk issuing from swollen metatarsal glands in the forelegs (Barth 1954; Alberti and Storch 1976). They live in silken tunnels constructed on surfaces of trees and other objects in the more humid regions (Fig. 2-1) and under rocks, bark flaps, or logs in the drier parts of their range. Webspinners display numerous adaptations for life beneath silk walls, including a flexible, slender body allowing quick movements and U-turns in tight spaces, flexible antennae that resist tangling in silk, and wings that fold along a crease that runs perpendicular to the length of the wing. This latter feature prevents their wings from catching in the silk as the males dart backwards (Ross 1970). Webspinners graze on the outer bark of trees, leaf litter, mosses, algae, and lichens on bark, rocks, mounds and soil (Ross 1970).
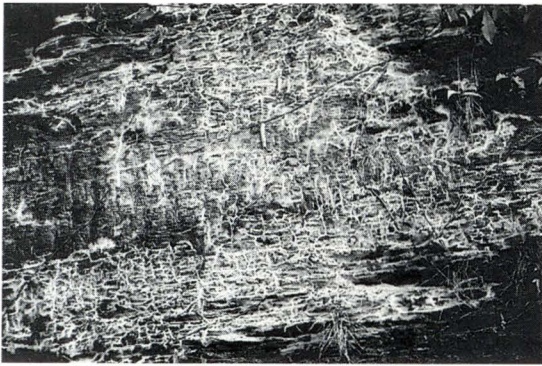
Fig. 2-1. Silk tunnels of an *Antipaluria urichi* colony, approximately 1 m wide, on a mud bank along a road cut in Trinidad's Northern Range. Photo.: J. S. Edgerly.

Ross successfully reared species, collected throughout the range of the order, on a diet of dry oak leaves and lettuce, a testament to their generalist requirements.

Observational evidence suggests a multifaceted function for silk, including shielding from abiotic factors as well as from predators, as proposed below. The outer covering of silk provides protection from heavy rain in the tropical habitats common to most embiids. Torrential rains trigger stemflow on trees supporting embiid colonies. After one such inundation in Trinidad, I tore open silk of colonies of *A. urichi* and discovered virtually dry substrate beneath the silk. I further investigated the wetting properties of silk by placing a section of a silk wall across the mouth of a jar, pouring water onto it from above; water did not penetrate the silk (Edgerly 1986). Silk may also shield inhabitants from direct sunlight and desiccation, although thermoregulatory properties remain to be investigated in the field.

Subsocial behavior in embiids

Maternal care

Maternal care has been observed in all embiids that have been closely examined. For example, adult females position their bodies over or near clustered eggs in *Anisembia texana* (Anisembiidae) (Mills 1932; Choe 1994), *Antipaluria urichi* (Edgerly 1987a, 1988), *Embia major* (Embiidae) (Imms 1913), *Oligotoma ceylonica* (Oligotomidae) (Bradoo 1967), *O. greeniana* (Bradoo and Joseph 1970) and *O. humbertiana* (Ananthasubramanian 1957). Some females also produce a complex egg mass, covered with substrate materials, silk, and/or fecal material (Imms 1913; Ananthasubramanian 1957; Bradoo 1967; Bradoo and Joseph 1970; Edgerly 1987a). In contrast, *O. ceylonica* produces a single egg per day for two to two and one-half months, laying them in linear rows in the silk (Bradoo 1967). After egg hatch, females stay with their nymphs, as reported for *Anisembia texana* (Mills 1932; Choe 1994), *Antipaluria urichi* (Edgerly 1987a, 1988), *O. ceylonica* (Bradoo 1967), *O. saundersii* (Ling 1935) and *E. major* (Imms 1913). Although maternal behavior appears ubiquitous throughout the order, its function has been investigated in the field only for *A.urichi* (Edgerly 1987a,b, 1988). In this case, females protect their eggs from egg parasitoids and provide silk for newly hatched nymphs (see below; Edgerly 1988). Bradoo (1967) noted that nymphs of *O. ceylonica* follow their mothers through silk tunnels, with newly hatched nymphs being especially tenacious. Laboratory observations of *E. ramburi* of the Mediterranean region revealed that females provide macerated food to nymphs (Denis 1949; LeDoux 1958), a relatively complex form of maternal behavior for an insect. Also striking was Ross' (1970) observation of an Afghan species, *Paedembia* n. sp., which harvests aromatic leaves of the shrub *Artemisia*, caching them in subterranean galleries. Providing food to young is a feature of other subsocial insects, including cockroaches (Seelinger and Seelinger 1983; Nalepa 1984), crickets (West and Alexander 1963), cydnids (Sites and McPherson 1982), dung beetles (see, for example, Halffter 1977), earwigs (Radl and Linsenmair 1991) and membracids (Wood et al. 1984) and may have promoted complex communication systems in some insects, as in passalids (Pearse et al. 1936; Schuster and Schuster, this volume) and *Nicrophorus* (Milne and Milne 1976). Embiids that provide food for offspring and that live in nest-like structures (whereby food is collected from the outside and brought into the silk tunnels) are of particular interest in a search for more complex societies within the order.

Males are not known to exhibit parental care, but because of limited observations such behavior cannot be ruled out. Of particular interest for future study are the many species with wingless males (e.g. all males in the family Australembiidae; Ross 1963) which may spend more time interacting with females, and perhaps with their young, within silk tunnels. For example, Melander (1903) frequently encountered wingless males of the dimorphic *Anisembia texana* living in galleries with females. However, because males of most species do not feed after reaching maturity and die soon after mating (Ross 1970), they appear to lack the longevity necessary for guarding eggs and nymphs.

Table 2-1. *Types of embiid colony*

Species	Solitary	Communal	Max. number of females	Number of colonies	Reference
Anisembia texana	×	×	6	—	Melander 1903[a]
Antipaluria urichi	×	×	24	143	Edgerly 1987, 1994
Embia major	×	—	1	130	Imms 1913
Oligotoma ceylonica ceylonica	—	×	39	—	Bradoo 1967[a]
O. humbertiana	×	—	1	—	Ananthasubramanian 1957[a]
O. saundersii	—	×	185	—	Bradoo 1967[a]

[a] Anecdotal report.

Tendency to live in groups

In addition to mother–offspring associations, field colonies of webspinners exhibit a variety of social groupings, varying from solitary individuals to females with young to combinations of solitary and communal groups to populations with apparantly obligate communal colonies (Table 2-1). Embiid life cycles vary from one generation per two years to up to five generations per year (Table 2-2). In species with many generations per year, overlap of generations within a colony is possible and may promote complex social interactions as yet undiscovered in webspinners.

Sex ratio

Although embiid sex ratios have not been studied in detail, anecdotal reports suggest variability within the order. The males' short adult lifespan and ability to fly may contribute to their relative rarity in collections of inhabitants within silk. Bradoo (1967) found for *O. ceylonica* seven adult males

and 28 adult females in a total of 28 field colonies: most of the 203 embiids collected were nymphs. In an intriguing statement, Melander (1903) reported that a single male develops from a brood of nymphs of *A. texana*. Ananthasubramanian (1957) reared 40 males and 31 females of *O. humbertiana* in the laboratory. The sex ratio in this case was not significantly different from 50 : 50 (Edgerly 1986). Similarly, Bradoo and Joseph (1970) reported an overall sex ratio for *O. greeniana* of 57 males to 46 females from five laboratory cultures.

Parasites, predators and inquilines

A suite of parasitoids has evolved that specialize on embiids. In some cases, these parasitoids may have promoted group living and/or maternal care, although few studies have tested such hypotheses. Sclerogibbidae (Fig. 2-2), a family of aculeate Hymenoptera, are ectoparasitoids of embiid nymphs (Callan 1939; Krombein 1979; Sheltar 1973).

Table 2-2. *Generations per year for five species of embiid*

Species	Location	Generations per year				References
		0.5	1	2	4–5	
Anisembia texana	Texas	—	×	—	—	Mills 1932 Melander 1903
Embia major[a]	Himalayas, India	—	×	—	—	Imms 1913
E. taurica	Crimea	×	—	—	—	Kusnezov 1904
Oligotoma ceylonica ceylonica[b]	India	—	—	—	×	Bradoo 1967
O. japonica	Japan	—	—	×	—	Okajima 1926

[a] Females lived up to 6.5 months after oviposition.

[b] Each generation was completed within 72 days.

Although I observed only two interactions, female *Antipaluria urichi* did not aid their nymphs when sclerogibbids entered their silk; the wasp's ability to sting may prevent the embiid from defending her offspring (Edgerly 1988). Indeed, one embiid female bolted from her silk covering in response to a lunging attack by a sclerogibbid. Scelionid wasps (*Embidobia* sp.) parasitize webspinner eggs (see, for example, Callan 1952) and may have played a significant role in promoting complex egg guarding as seen in *A. urichi* (see below). Other parasitoids attack mature embiids. For example, tachinid flies parasitize *Clothoda* in Peru (Arnaud 1963) and *Dictyoploca* in South Africa (Mesnil 1953). In addition, a newly discovered genus of braconid, *Sericobracon* Shaw, utilizes *Antipaluria* adults as hosts in Trinidad (Shaw and Edgerly 1985). Disease organisms such as gregarines (*Gregarina marteli, Diplocystis clarki*)

Fig. 2-2. A sclerogibbid female, *Probethylus callani*, walking on a silk wall of *Antipaluria urichi*. The abdomen of an embiid nymph, the wasp's host, is visible through the silk. Photo.: J. S. Edgerly.

(Stefani 1959, 1960) and coccidia (*Adelea transite*) (Denis 1949) also infect embiids. Interestingly, Stefani (1959) suggested that a protozoan, *Diplocystis clarki*, effectively sterilizes males in *Haploembia solieri*, leaving residual parthenogenetic populations in parts of Italy. The impact of these parasitoids and disease agents on the evolution of communal behavior in embiids has not been studied.

Predation is also a source of mortality for embiids, both within and outside of silk. In Trinidad, I observed ants, spiders, geckos, and a neuropteran larva (Ascalaphidae) killing *A. urichi* that were wandering outside of their silk (Edgerly 1988). In addition, Callan (1952) observed an asilid fly preying on this species. Other predators (ants) reach embiids by cutting through silk, pulling off sheets of silk (birds), or piercing through it (harvestmen, Edgerly 1988, 1993; reduviids, Denis 1949). Below I describe results of my investigation of the differential risk of predation for individuals in different-sized colonies, a possible selective agent maintaining facultative communal behavior in this species.

The silk of webspinners provides a habitat for embiophiles in the heteropteran family Plokiophilidae. The relationship between these bugs and their hosts is unclear: they may act as predators on embiid eggs or young nymphs (Callan 1952) or other insects and mites within the silk, or as scavengers on carcasses or scraps of material within the gallery (Carayon 1974). In *A. urichi*, plokiophilids occurred in 62 of 80 field colonies (Edgerly 1987a). Webspinners also live within silk of other embiid species; I observed *O. saundersii* inhabiting galleries of *A. urichi* in Trinidad (for similar examples from India, see Mukerji 1928). The outcome of such interactions is not understood. Perhaps even more surprising are the embiids (*O. ceylonica*, Bradoo 1967; *O. greeniana*, Bradoo and Joseph 1970) that live within colonies of the social spider *Stegodyphus sarasinorum*, where they appear to feed on algae growing on the spider silk. Bradoo suggested that webspinner silk protects embiids from being detected by spiders. In addition, I discovered two species of webspinners (*Diradius* n. sp. (Teratembiidae) and *O. saundersii*) living on the surface and within the outer fabric of termite nests (*Nasutitermes*) in Trinidad; the embiids apparently graze on algae and/or lichens on the termite nests. Soldier termites did not respond to webspinners that remained within their silk; however, when I opened the silk with forceps, the exposed embiids quickly elicited an alarm response from the termite soldiers (Edgerly 1986). Other embiid species have also been observed in close association with termites (references in Imms 1913).

CASE STUDY: RESEARCH ON *ANTIPALURIA URICHI*

Habitat and life cycle

Locally abundant, *A. urichi* is restricted to Trinidad (Ross 1987), an island situated approximately 11 km off the coast of Venezuela. I conducted my study in the tropical rain forest of the Northern Range at the Simla Research Station and Asa Wright Nature Center. Females are relatively elongate for a webspinner (1.6 ± 0.015 cm (SE)); the winged males are typically shorter in length (1.2 ± 0.02 cm) (Edgerly 1987a). Their silk galleries are generally found on tree surfaces and vertical banks along road cuts (Fig. 2-1), but also on posts, concrete walls and flower pots. Silk covers their resting sites and feeding zones at the colony's edge where fresh algae and other epiphytes are found. Once

food is depleted, more silk is added, extending the forager's reach into unexploited sites. Resting sites remain fairly stable, often within a central location, as silk walls are expanded to enclose more feeding sites (Edgerly 1986). Ultimately, depletion of food may trigger dispersal from a colony site. Although webspinners typically do not venture outside their silk, one can see them by peering through new, thin silk as they graze on algae at night at the outer perimeters of the silk covering.

I concluded, by observing marked females and colonies, that the reproductive cycle of *A. urichi* is aseasonal; reproductive females were present every month I observed them, which included all months except April, May and June (Edgerly 1988). Embryonic development takes approximately 6 weeks; nymphal development requires 18 (Edgerly 1988) (Fig. 2-3). A key feature in more highly
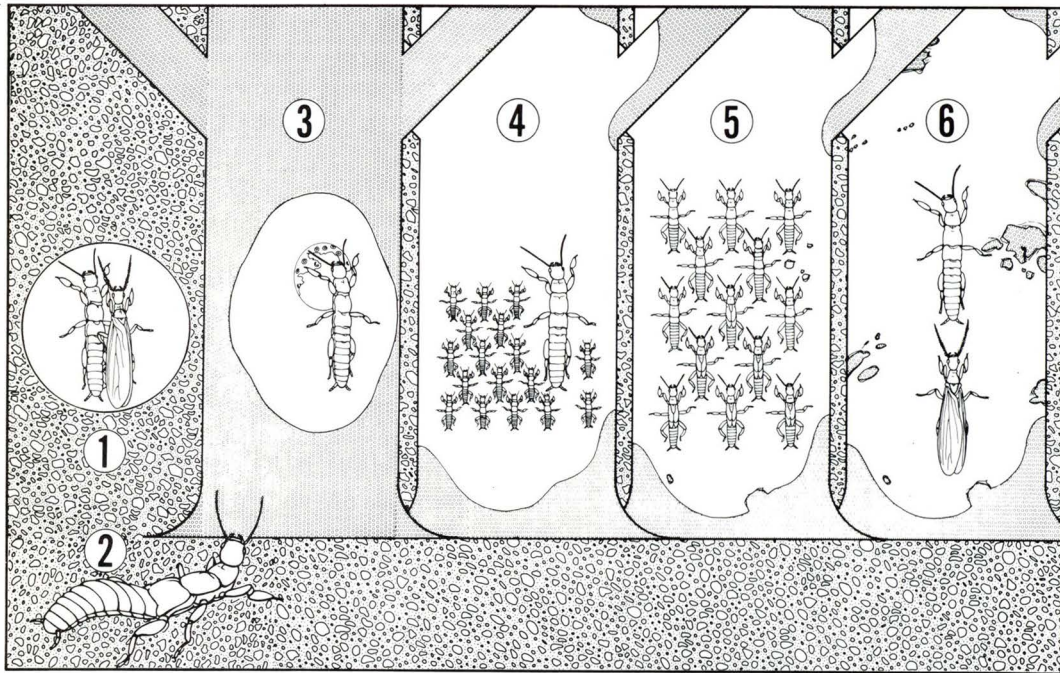

Fig. 2-3. Life cycle of *Antipaluria urichi* in Trinidad. Each number on the drawing represents a different point in the life cycle. Time is along the horizontal axis: each consecutive, diagrammatic tree to the right shows the same colony, only older. (1) Mating occurs within silk. (2) Dispersal often occurs in this species, from the natal colony to another tree or within the same tree, although the exact timing relative to reproduction is not known. (3) Egg-guarding by an adult female, requiring approximately six weeks. The white area represents silk spun by this solitary female; the circular object beneath her is her egg mass hidden under an egg mass covering. (4) The number of nymphs shown is the average number observed in field colonies. The female increases her silk-spinning activities as reflected in the larger expanse of silk. (5) The adult female generally disappears when the nymphs are approximately half grown. The nymphs also begin to disappear as they grow, as reflected in the fewer individuals in the colony. (6) Here only two mature embiids are left, 18 weeks after hatch. The silk shows many tears that have accumulated. For details used to produce this drawing see Edgerly (1986, 1987a,b, 1988). Drawing: Edward C. Rooks.

social insects, the overlap of generations within the nest, is apparently lacking in *A. urichi*. All adult females disappeared or died at varying times before their offspring matured (Edgerly 1988). Furthermore, only two of 15 closely monitored colonies produced female offspring that matured and reproduced in their natal colonies; all others disappeared. The structure of their life cycle lacks other factors that may favor more complex interactions, since individuals typically disperse prior to reproducing and do not interact with distant generations.

Maternal care

Egg-guarding behavior

As in many other subsocial insects (references in Wilson 1971; Eickwort 1981; Tallamy and Wood 1986), female embiids attend to clustered eggs until hatching, and subsequently remain with their nymphs. By employing focal sampling techniques, I determined that females invest approximately 85% of their time in egg attendance and care during the six-week developmental period (Edgerly 1987a). Such activities include spinning silk on the egg mass, positioning her body over the eggs while actively turning her head, and vigorously shaking and lunging at approaching plokiophilids, scelionid wasps, or other webspinners. These guarding behaviors persist day and night. Such activity is in sharp contrast to that displayed by pre-reproductive females and females with nymphs, who generally sit still during the day, and move, feed and spin silk at night. A cost of such maternal care is the inability of egg-guarding females to feed as often as other individuals. Their investment goes beyond behavioral protection, for they also provide physical protection by constructing an elaborate egg mass covering of macerated bark and other substrate materials, silk and possible salivary secretions that together produce a tough outer coating on each egg. After each egg is coated in this manner, the mother affixes it, with her other eggs, to the substrate, yielding an egg mass of 53 ($\pm$2.7) eggs, on average (Edgerly 1987a). After oviposition, the mother adds macerated materials and silk to the top of the compact egg mass. The egg mass covering functions, at least in part, to prevent successful oviposition by scelionid wasps, which have difficulty penetrating the covering. The delay caused by the wasps having to dig and probe for eggs allows adult embiids time to repair their silk galleries and to feed at the perimeter of the silk covering without risking parasitism during their absence from the eggs.

Guarding females are effective in protecting most of their eggs from parasitoids, as revealed by experimental results where naturally occurring field eggs from which females were removed suffered significantly lower hatching rates ($12.9 \pm 8.7\%$) than did neighboring guarded eggs ($71.1 \pm 8.3\%$) (Edgerly 1987a). The lower hatch rate of unguarded eggs was due to parasitism by scelionid wasps and predation by ants.

The egg mass covering may protect eggs from desiccation in the dry season or fungal infestation in the rainy season. In order to test these ideas, I placed egg masses with approximately one-half of the covering removed in parasitoid-exclosure bags in the field or in Petri dishes in the laboratory. Even though approximately the same number of nymphs hatched from uncovered (treatment) and covered eggs (controls), 56% of those hatching from control eggs died entombed beneath the egg mass covering. After discovering this potentially lethal impact of the egg mass covering, I observed females more closely and discovered that at approximately six weeks after oviposition they remove the egg mass covering with their mandibles, thereby facilitating hatching. Similar behavior has been observed in spiders which open their egg sacs to facilitate spiderling emergence (references in Horel and Gunderman 1992). If a female embiid is killed prior to emergence of her nymphs, her eggs risk death by parasitism or emergence failure because of the egg mass covering. Parasitoids are ubiquitous (79% of 67 colonies housed egg parasitoids) and represent an almost constant threat to eggs; these scelionids are able to parasitize at any time during the egg's developmental period. The chance of eggs being abandoned, however, appears to be relatively low (18% of 44 females with eggs), and hence, the negative consequences of emergence failure because of the egg mass covering are rarely realized.

Maternal care of nymphs

After their eggs hatch, females invest significantly more time in behaviors displayed prior to their stint of egg guarding: spinning silk, feeding and moving within the galleries at night, and resting during the day (Edgerly 1987a). Females with nymphs may provide an important commodity for their developing young, as evidenced by an exponential increase in area of the silk covering after hatch. In contrast to *E. ramburi* (Denis 1949; LeDoux 1958), female *A. urichi* do not feed their nymphs, but, rather, feed alongside them at the periphery of the silk covering.

The mother's presence increases the development rate of the offspring (Edgerly 1988). The cause of the deficit in developmental rate when the mother is absent has not been clarified experimentally, but may be partly due to an increase in silk spinning by nymphs to counter the lack of maternal silk, which generally forms a dense outer covering. Choe (1994) discovered similar slow development in orphaned *Anisembia texana* nymphs in a laboratory experiment. Here, too, the nymph-produced silk covering was relatively thin.

Antipaluria urichi also exhibit hygienic behaviors, gathering fecal pellets into piles and silking them into the sides of their galleries. Other species have been observed gathering fecal pellets and pushing them through the silk wall to the outside (Ling 1935). Interestingly, E. S. Ross (personal communication) suggested that, in the tropics, feces pushed onto the silk surface serves as a substrate for microflora that may further enhance a colony's cover. Adult females may more effectively perform these activities, although the function of fecal handling remains to be tested. A similar observation was made on female subsocial crickets (*Anurogryllus muticus*) (West and Alexander 1963), and earwigs (see, for example, Radl and Linsenmair 1991), which remove excess waste material and fungi from underground burrows.

Comparison with other subsocial insects

Many species of insect guard their eggs against predators by utilizing chemical or other defensive behaviors. For example, lacebugs attack predators by fanning their wings and rushing at them (Tallamy and Denno 1981). *Antipaluria urichi* do not attack predators, other than intruding embiids, that threaten their eggs. Ants sometimes enter silk and destroy entire egg masses, while female webspinners retreat in response (Edgerly 1988). They apparently lack defenses against predators that easily sting and dismember an adult embiid, a soft-bodied insect. Embiids do, however, gain protection by producing silk walls, which, if intact, usually evade detection. Ants march along trails directly on webspinner silk, without attacking the occupants (E. S. Ross, personal communication; Myers 1928; Denis 1949; Edgerly 1988). If, however, the silk covering is breached, detection is afforded, and ants will enter and attack (*O. saundersii*, E. S. Ross, personal communication; *A. urichi*, Edgerly 1988).

Living within silk may protect *Antipaluria*, but it also concentrates their eggs, thus increasing the risk of annihilation if discovered by egg parasitoids or predators. Under these conditions, the resultant strong selective pressure exerted by egg parasitoids may have promoted the relatively elaborate behaviors associated with maternal care in *A. urichi*. For future work, a systematic comparison of embiids that vary in their tendency to construct egg masses (references in Edgerly 1987a) may reveal to what degree egg mass coverings and egg guarding are associated.

In their assessment of convergence in subsocial insects, Tallamy and Wood (1986) concluded that factors favoring the origin of parental care include reproduction confined to specific periods and places, extended adult longevity, and basic behavioral elements that can be molded into defensive posturing or nest building. The authors also suggested that an insect's association with a particular nutritional resource may promote parental care. According to their scheme, *A. urichi* resemble foliage feeders because of their surface-feeding tendencies. Hence, their exposure to predators as they feed may have promoted antipredator behaviors, such as production of the silk covering. Their relatively long adult life and pre-existing defensive behaviors as seen when they fight with intruding embiids – shaking, lunging and biting – may have further promoted the evolution of parental care. Egg-tending embiids use these same behaviors when encountering scelionid wasps or other webspinners near their eggs.

Insects in the Order Psocoptera exhibit behaviors observed in webspinners with some interesting differences. Psocids, commonly called bark lice, often spin conspicuous webs on bark where they feed in a manner similar to embiids: they add silk to cover new feeding sites, depleting food as the colony expands. Psocopteran silk shields against ants and other predators (references in New 1973), as suggested for webspinners. Colonies often form by convergence of groups derived from different founding females on the same tree, again reminiscent of webspinners. Unlike embiids, most psocids are not subsocial, however; only a few families contain species exhibiting maternal care and/or gregarious behaviors. According to Mockford (1957) group-living in psocids varies as follows: nymphs live in small groups under loose webs; nymphs live in large herds, which break up soon after they reach adulthood; females stay with eggs, but usually die prior to hatch; and, showing the highest degree of sociality, nymphs emerge in webs made by their mothers or by both parents plus their siblings. In this last type, found in the genus *Archipsocus*, nymphs stay in their natal colony and contribute to the webbing, as well as repairing it when torn. Some of the parental generation may be alive when

the nymphs reach adulthood, so that generations may overlap within the colony. Species in the Family Archipsocidae often have hundreds of psocids sharing a silk sheet that they spin together over bark and other substrates. The tendency to aggregate may be associated with silk-spinning, although one species, *Peripsocus nitens*, does not produce conspicuous webs, and yet appears to exhibit an intriguing phenomenon of communal oviposition. Female *P. nitens* stay with their eggs, often in clusters consisting of eggs numbering up to a few hundred produced by a number of females. They perhaps care for their eggs in some way (New 1985). The behavior is reminiscent of lace bugs, which add their eggs to other females' egg batches, thereby exploiting the care-giving of the receiving female. The egg-dumping lace bug leaves her eggs with another female, commences feeding, and ultimately produces more eggs (Tallamy 1985). The lace bug that receives the extra eggs may gain an antipredator advantage for her eggs via the dilution effect, or because her eggs gain safety by being in the center of the egg mass. It remains to be determined what advantage a female *Peripsocus* gains by clustering her eggs with hundreds of eggs produced by neighboring females. Protection against parasitism appears not be the function of maternal care here, however, because egg parasites seem rare for *P. nitens* (New 1985), a striking difference from what I observed for *Antipaluria*.

Given the similarities in silk-spinning and feeding behaviors of Psocoptera and Embiidina, it would be interesting to determine what factors contribute to the differences in their tendency to exhibit subsocial behaviors. Although maternal behavior occurs in psocids, it appears rare, limited to few species within the order. This is in contrast to the embiids, all of which appear to exhibit care of their eggs. Factors promoting such differences remain a puzzle but may include the high incidence of egg parasitism and perhaps egg cannibalism within webspinners. A closer comparison of the two orders, requiring more intensive field work, seems worthwhile.

To help complete the picture of evolution of embiid subsociality, the behavior of subterranean webspinners should be investigated further. These species may more closely resemble earwigs, burrowing crickets (references in Tallamy and Wood 1986), and others that suffer from threats not associated with surface feeding, such as infestation by fungi or other soil contaminants. Behavior in these species may be more complex than in *Antipaluria*, especially if females gather food from outside, returning it to offspring in a silk nest.

Communal behavior

Description of colonies
The facultative communal nature of *A. urichi* allows for the comparison of attributes associated with reproductive success for solitary females with their offspring, to those in colonies with as many as 72 individuals, including up to 24 adult females. Surveys of colony occupants in different areas in Trinidad in 1984 revealed variation from as many as 86% of the females being communal (of 138 females in 44 colonies), one colony with 9 egg masses, to 37% being communal (of 57 females in 64 colonies) (Edgerly 1986; 1987b). Individuals sharing silk hatch within the colony or enter as immigrants. Based on observations of marked individuals I inferred that relatedness of colony-mates varies from mother–offspring associations to groups of unrelated individuals that joined each other to combinations of the two types. No analysis exists determining relatedness within a colony or on a tree, which may be high given the limited ability of wingless females to disperse over long distances (Edgerly 1987b). I documented a pattern of recruitment of new silk galleries on trees that suggests that dispersers remain on their host trees, establishing colonies close to their mothers' colonies, rather than crossing the forest floor to disperse to other trees (Edgerly 1987b). However, at least for most webspinner species, males fly in search of mates, potentially reducing relatedness of neighboring individuals. Relatedness within colonies needs to be examined in embiids; species of particular interest are those with more sedentary, nymph-like, wingless adult males (e.g. *Paedembia*) (Ross 1970).

Consequences of group-living
Impact of parasitoids. An advantage of group-living in *Antipaluria* is enhanced egg production by communal females (Edgerly 1987b). However, egg parasitoids reduce this bonus, so that ultimately communal females produce the same number of hatched eggs as do solitary females. A key predictor of egg parasitism rate is how close egg masses are to each other on a tree; the closer they are, the greater the chance of parasitism. Furthermore, given egg masses of equal distance from one another, those produced in a communal colony suffer greater parasitism rates than do those produced by solitary females (Edgerly 1987b). Not only might egg parasitoids be differentially attracted to aggregated hosts (Hassell 1978), they may also hatch from eggs within a colony and search therein for nearby

egg masses. The scelionid's ability to oviposit into eggs at any point in egg development heightens the risk of having parasitized eggs nearby. Ecological factors promoting differences in egg production for communal and solitary females remain unknown. They may include an increase in energy expenditure by solitary females that may spin more silk or walk further to distant sites when establishing a gallery. Such dispersal may be adaptive because females colonizing distant sites appear less likely to attract scelionid wasps (Edgerly 1987b), but may reduce their ability to produce as many eggs as they might have had they stayed close to their natal site. Furthermore, enhanced fecundity in communal females may not be due to benefits of social interactions *per se* but rather to site-specific resources, which elicit colonization by many females. In a laboratory study, LeDoux (1958) found that grouping by embiids may be partly in response to favored food resources. He observed that 15 *E. ramburi* initially fought when placed together, but over a two-week period showed a marked tendency to form silken tubes together in the vicinity of their food.

Impact of predation. Differential predation on colonies of varying sizes may maintain the facultative communal system of *Antipaluria*, whose colonies vary in expanse of silk covering, as well as in number of occupants. Recently (Edgerly 1993), I tested whether the probability of a predator detecting a colony increases proportionately with an increase in expanse of silk. Larger colonies would not gain an antipredator benefit from grouping if this were so, unless other attributes, such as group defense, enhancement of silk as a protective layer, or the dilution effect, served to protect them (see, for example, Foster and Treherne 1981; Turchin and Kareiva 1989). The predator avoidance effect hypothesis of Turner and Pitcher (1986; see also Dehn 1990; Inman and Krebs 1987) predicts that, in fact, larger groups are not proportionately more likely to be encountered by visually hunting predators. Using observational techniques, I determined that there was a less than one-to-one relationship between attack rate and increase in size of the colony. Holes cut in the silk increased during a three-week study at a rate of only 0.12 holes added per square centimeter of silk as the silk wall perimeter increased. Therefore, from the predator's point of view, less expansive silk walls are more conspicuous than their size would suggest; predators directed proportionally more attacks at smaller silk walls than would be predicted by their relatively small size. Webspinners, therefore, may be safer

when housed under larger sheets of silk because of the lower attack rate per unit area relative to that experienced, on average, by smaller colonies. The impact of conspicuousness of silk on predation rates may not fully explain differential predation risk; further analysis is required to determine whether crowding within a colony promotes safety in numbers via the dilution and/or confusion effects.

Although not yet investigated, vibratory signals through silk may enhance webspinner defensive responses by providing a warning of predator attacks elsewhere in the colony, as has been recently reported for spiders (Uetz and Hieber 1994). Reception of local vibratory signals in embiids seems likely because of the unusual stance adopted within their galleries: their first and third pairs of legs rest ventral to the body, while the middle pair is hooked dorsally into the silk. Any movement of silk could be perceived from above or below the animal. Furthermore, embiids appear to communicate by generating local vibrations by shaking rapidly, especially when an individual enters the gallery of another (Edgerly 1986; for *Anisembia texana*, Choe 1994).

In sum, costs and benefits of communal behavior may fluctuate depending on the age of the colony. Older colonies may suffer from heavy parasitoid loads (Edgerly 1986) and perhaps depleted food resources, but, on the other hand, may benefit from expansive silk walls. Furthermore, the larger number of individuals in older colonies may contribute to a potential dilution effect or other antipredator devices, and/or other attributes not yet determined.

Interactions between individuals. Aggressive interactions are common within *Antipaluria* colonies (Edgerly 1986), and have been reported for other webspinners as well (Ling 1935; LeDoux 1958; Bradoo and Joseph 1970; Choe 1994). Fights occur when dispersers cut into silk walls and enter established colonies. Webspinners respond to intruders by biting, pushing head-to-head, locking mandibles, and shaking vigorously. In experimental trials (Edgerly 1986), nymphs, adult females alone, and females with eggs were particularly responsive to intruding females. Females with nymphs, on the other hand, did not fight. Aggressive reactions generally did not cause the intruder to leave the silk; of 20 trials, 16 ended with the intruder staying. These experimental results paralleled field observations revealing that dispersers often join existing colonies, despite the sometimes aggressive reactions of residents (Edgerly 1987b). Fighting most likely results in spacing individuals

out within the colony rather than pushing them out completely. Once established within a silk gallery, adult females rarely interact much beyond adding silk to, and sharing, contiguous silk walls.

Further studies are required in order to determine the function of fighting and why aggressive tendencies vary. One possibility is that females joining a colony are a threat to eggs (Edgerly 1986). In an preliminary attempt to determine whether females can recognize their own eggs, I moved marked females (maternal females; $n = 17$) from their own egg masses to other egg masses within their own or in neighboring colonies. In addition, I placed adult females without eggs (non-maternal; $n = 3$) onto egg masses to see if they would guard, abandon, or consume them. Ten of the maternal females relocated their own eggs and resumed guarding, one assumed a guarding posture over the adopted eggs, and the six others disappeared. The non-maternal females maintained their new positions, and consumed at least half of the eggs within two days of introduction to each site. Two of these egg masses were eventually completely consumed; the third was abandoned because of predation on the female. Other possible factors promoting the evolution of aggressive responses, yet to be examined, include risk of cannibalism for molting nymphs and risk of increased conspicuousness to parasitoids for closely grouped embiids.

CONCLUSION

Webspinners remain one of the least understood orders within the Class Insecta. Embiids appear to exhibit variation in parental behavior, but such variation has not been well documented. Furthermore, their tendency to live in groups also appears to vary; variability that is worth investigating. Of particular interest are species with dimorphic males, and especially those with nymph-like males. Males, in such species, may contribute to care of the young, or guard their mates. As revealed in this chapter, group living occurs within the order, but only one species, *A. urichi*, has been studied in detail in the field, and for that species many questions remain, such as: What role do the ubiquitous hemipteran inquilines (family Plokiophilidae) play? Does the dilution effect promote living in groups? and; Do females gain an advantage from sharing silk? In addition, the possibility of greater social complexity within the order is also an intriguing question. Subterranean species that store food in chambers, such as *Paedembia* n. sp. discovered by Ross in Afghanistan, may exhibit

more complex social interactions than seen in *Antipaluria*. Because the former collect food to stock their nests, generations may overlap within the colony, as they do within the Hymenoptera. In contrast, *Antipaluria* colonies slowly deplete algae from their natal colony sites perhaps triggering dispersal so commonly observed in this species. Nest-sharing in *Paedembia* and in other embiid species like them may facilitate more complex systems of communication and other social interactions. The harsh climate of Afghanistan, the difficulty of forming nests underground, and the unpalatability of their food (sagebrush leaves) resemble extrinsic factors proposed by Evans (1977) to promote the evolution of higher sociality. At the other end of the social spectrum, adult females in an African species discovered by E. S. Ross (personal communication) are intolerant of each other and extremely aggressive. Uncovering ecological correlates of such behaviors may yield answers concerning the evolution of communal behavior within the order.

The evolution of insect parental behavior also warrants closer inspection, for it appears in many orders of insects. If all webspinners are subsocial, as has been suggested by Ross (1970), then an examination of the order's sister group may help in discovering roots of parental care. A more difficult problem in analyzing the evolution of parental care in webspinners is the lack of a widely accepted phylogeny for orthopteroid insects. Because all embiids are subsocial, comparisons with asocial relatives would require identification of a sister group. Despite these difficulties, one could compare maternal investment for speices within the order with differing life history strategies (iteroparity vs. semelparity) or differing colony locations (arboreal vs. subterranean or beneath rocks) to determine what ecological factors promote heavy investment in a single brood. In addition, as suggested above, comparisons with insects in the Order Psocoptera may also help address questions of selective pressures that led to the evolution of subsocial behavior within the embiids, and more rarely within the psocids.

In conclusion, most important for future research will be basic field observations and quantitative analysis of behavior in as many webspinner species as possible, preferably from a variety of families and habitats. Such studies will add tremendously to the scant information that exists in the literature at the present time. Trends within the order cannot be identified without such information. Finally, phylogenetic analysis is still needed, and many newly discovered species remain to be described (E. S. Ross, personal communication).

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