Behavior and Reproductive Status of *Microsepsis armillata* (Diptera: Sepsidae) Flies Away from Oviposition Sites

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ABSTRACT The mystery of where virgin female *Microsepsis armillata* (Melander & Spuler) copulate has been solved with the discovery of sexual activity in small aggregations that are not tightly associated with the oviposition sites, where matings have been observed previously in this and other sepsid species. Nonvirgin females also mate in these aggregations, and matings at such sites may help explain the otherwise puzzling variations in male precopulatory riding behavior in other sepsids. Approximately 25% of the unpaired females in aggregations carried an unlaid egg in her bursa, and larvae had hatched from some of these eggs. Retention of a bursal egg could prevent intromission by males.

KEY WORDS *Microsepsis armillata*, mating, aggregations, virgin females, Sepsidae

SEPSID FLIES ARE characterized by an unusual mating system. Males wait near oviposition sites such as dung or carrion (Pont 1979), and mount females when they arrive. But the males only mate with females after oviposition is finished (Parker 1972a, 1972b; Ward 1983; Eberhard 1999; Schulz 1999). The morphological fit between male and female genitalia during copulation (Eberhard and Huber 1998) suggests why copulation is generally postponed until oviposition is completed (Eberhard 1996). Males of *Archisepsis* spp. and *Microsepsis* spp. deposit a large spermatophore that fills the anterior portion of the female's bursa, where each egg must pass on its way toward the ovipositor. At least in *A. diversiformis* (Ozerov) and *M. armillata* (Melander & Spuler) sperm transfer from the spermatophore to the female's spermathecae and spermathecal ducts is not immediate (unpublished data; L. Rodriguez, personal communication). Thus, if a male were to copulate with a female before she finished laying the mature eggs in her ovaries, his spermatophore would be driven out of her bursa by the next egg as it passed down her reproductive tract, and little or no sperm would be transferred. Alternatively, if a newly deposited spermatophore is difficult to displace, the female would be prevented from laying further eggs until she dislodged the spermatophore.

A pair of puzzles regarding sepsid sexual biology are associated with this mating system. First, a female's initial mating must occur before rather than after her first oviposition bout (Pont 1979). Yet published descriptions of mating only mention copulations following oviposition, so the many observations of matings by females just after oviposition leave unanswered the question of where a female's first copulation occurs (Hafez 1947, Foster 1967, Parker 1972a, Ward 1983, Ward et al. 1992, Zerbe 1993, Allen and Simmons 1996, Blanckenhorn et al. 1999, Schulz 1999). A possible solution is suggested by observations of occasional mating pairs of *Sepsis* in large aggregations (Pont 1987) and among flies in smaller groups away from dung (Schulz 1999), and a brief note on apparent mating attempts by *S. neocynipsea* Melander & Spuler at an apparent feeding site (Eberhard 1999). The current article presents a detailed study of reproductive behavior away from oviposition sites.

A second puzzle is that in some species, the males of some populations but not others ride the female before mating, thus apparently defending her against other males (Schulz 1999). The reproductive payoffs to the male from this type of defense are probably strongly affected by both the likelihood that the female will eventually mate with him after he has ridden her, and whether she is likely to mate subsequently with another male away from this site before she lays her next clutch of eggs. Mating does not always occur after riding in at least some species (40% and 92–97% of riding males failed to copulate in *S. cynipsea* (L.) and two species of *Archisepsis*, respectively (unpublished data; Parker 1972b). Subsequent matings away from oviposition sites could also be important, especially if the nearly complete second male sperm precedence documented in *S. punctum* (F.) (Schulz 1999) proves to be generally true for sepsids.

One possible type of mating site is a large aggregation such as those sometimes observed away from oviposition sites (Pont 1979, 1987). Some aggregations in England were huge, containing up to possibly 100,000 *Sepsis fulgens* Meigen flies (Pont 1987). Aggregations this large are not often encountered, however, and detailed behavioral observations of flies in them have never been made. It appears that most individuals in these aggregations neither feed nor engage in sexual interactions (Pont 1979, 1987). Another possible site of mating is a smaller group, such as the

flies associated with resources such as food or water. Katja Schulz (personal communication) reported aggregations of *S. neocynipsea* with a few *S. punctum* along streams and in moist meadows in the mountains of Arizona, and has also seen mating in several species of *Sepsis* at older dung, which serves for feeding but not oviposition. Silva (1993) mentioned that adults of *Palaeosepsis* sensu latu (includes *Archisepsis* and *Microsepsis*) have been captured on grasses, apparently away from dung or carrion.

The current study uses behavioral observations and dissections to determine both the reproductive condition (ovary development and spermathecal contents) and the recent feeding history (intestine contents) of females of *M. armillata* captured away from oviposition sites. Additional fragmentary data are given for *M. mitis* (Curran) and *A. discolor* (Bigot).

Materials and Methods

Observations were made in pastures and early second growth (shrubs and small trees) near San Antonio de Escazu (elevation 1,400 m), San José Privince, Costa Rica between December 1998 (just before the beginning of the dry season) and the end of April 1999 ($\approx$2 wk into the next wet season). Brief observations were also made on 10 and 11 April $\approx$5 km W of Atenas, Alajuela Province, Costa Rica. Counts of flies were performed while walking or crawling very slowly to minimize the number of flies disturbed. Only flies $\approx$0.5–1.5 m ahead were counted, and flies that were seen landing (some of these were undoubtedly stirred up by my movement) were not counted. The flies' tendency to spend nearly all their time on the upper rather than lower surfaces of leaves or other planar surfaces, and to fan their wings and walk about actively made it likely that this survey technique included the large majority of the flies present, despite their small size ($\approx$3–4 mm long). Flies were collected either by aspirating individuals or by swinging an insect net over their resting place.

Aggregations were distinguished from scattered individuals somewhat arbitrarily. An *aggregation* included a central area where there were several leaves with at least 3–4 flies per leaf, and where interactions between individuals occurred frequently. It is possible that some flies judged to be scattered rather than in an aggregation actually belonged to an aggregation whose center was missed. My search for flies was focused on the upper surfaces of leaves <1 m above the ground. Because two other species of *Microsepsis* and a similarly sized species of *Archisepsis* were also present in both study areas, all species identifications were made by collecting flies and examining them under a dissecting microscope. Confident identifications were only possible for males and for females that were captured with a mounted male. Females of *A. armata* near Atenas, and of *A. diversiformis* near San Antonio de Escazu were also identifiable because at each of these sites this was the only species with dark spots on the wings. Probable identifications as *M. armillata* of unpaired females that were dissected was

made when the female fulfilled two conditions: she was found in an aggregation in which 90–100% of the males that were collected on the same or previous days were *M. armillata;* and she was larger than the median size of all females collected from the same site. Because the other species found in these aggregations, *M. mitis*, is smaller on average than *M. armillata*, selection of larger females for dissection made it very probable that they were *M. armillata.*

Females to be dissected were either placed in 70% ethanol and dissected within a day, frozen and then dissected in saline solution, or placed in a refrigerator at $\approx$5°C (where they were completely immobile) for 1–2 d and then dissected in saline. I noted the following: (1) the relative volume and color of the contents of the enteric cecae or crop, and of the two loops of middle intestine lying between the two ovaries; (2) the contents of the vagina (spermatophore, egg, male genitalia, empty); (3) the length of a large egg in the ovary; (4) the relative degree of filling of the large and small spermathecae with sperm (judged by isolating the spermathecae on a slide, squashing them under a coverslip, and observing sperm density under a compound microscope); and (5) the relative development of the ovaries, including both relative sizes of eggs and of the ovary itself (judged on the basis of the range of development seen in dissections for a previous study) (Eberhard and Huber 1998). Ovaries of females collected while copulating on dung and that had just laid a clutch of eggs were judged to be $\approx$20% developed. Females with no sperm in either spermatheca were presumed to be virgins. Sample sizes differed for different structures, as some structures were not examined in some dissections. Means are followed by $\pm$1 SD.

Results

I found six aggregations of *M. armillata* that contained from $\approx$50 to >2,000 individuals. Most flies in aggregations were on the upper surfaces of more or less horizontal leaves <15 cm above the ground. Many species of plants were occupied, and leaf sizes varied widely (from <1 to >1,000 cm^2). Maximum densities were only 1–2 flies per square centimeter, and occurred only on a few, relatively small leaves. The largest aggregation was spread along $\approx$30 m of a small stream. Although some aggregations persisted for more than a month, they were not stable at a small scale. In two aggregations in an abandoned coffee field, for instance, both the number of flies and the central area where most flies were present changed from day to day.

All sites but one were at least partially forested, but were near the edges of open pastures. The exception was at the edge of a tree-lined path between shaded coffee fields where there were many fallen fruits of *Stemmadenia obovata* (Hook & Arm.). Three of the four aggregations found and observed repeatedly during the latter part of the dry season (March, early April) were near tiny streams whose width was as small as 15–30 cm in places. The largest of these ag-

gregations (near Rio Agres) had vanished on 27 April, ≈1 wk after the rainy season began, and the other two stream-side aggregations were also gone when they were checked the next day. In contrast, two aggregations that were found early in the dry season (December) away from water (at least 100 m from the nearest creek) disappeared later in the dry season. In no case were the flies nearly as densely clumped (so that the plants appeared black with flies) as the aggregations of *Sepsis* described by Pont (1979, 1987).

It was usually not obvious why one portion of an aggregation was more densely populated than others. In two cases with dense groups on leaves near water, however, I found a rotting fruit of *S. obovata* nearby with 10–30 flies resting on it. The flies in a third aggregation were within 3–5 m of a smashed, soft, and probably rotting root of a large aroid (probably *Xanthosoma*) in the water. Flies on rotting fruit frequently appeared to be feeding because they repeatedly tapped the fruit with their extended mouthparts. One female also apparently oviposited, because she extended her ovipositor with an egg visible inside, inserted it into the fruit for several seconds, and then finally pulled rearward with the ovipositor as if pulling the egg's long respiratory tail from her body (Ward et al. 1992, Schulz 1999). This female's identity as *M. armillata* was confirmed by raising her offspring. Oviposition behavior in an aggregation was not seen in any other case, however, so it is probably rare. Another aggregation was ≈2 m from a plant with a large population of membracids. The feces of the membracids accumulated on some leaves and under the plant, and were apparently fed on by several species of insects as well as by males and probably females of *M. armillata* and *M. mitis.* I cannot rule out the possibility that at other aggregations I missed attractants such as small feces or small dead animals under the leaf litter.

Scattered individuals were also found at three other sites. Males of *M. mitis* were relatively more common among these individuals. Among 21 scattered males collected on a hillside near a pasture, 90% were *M. mitis* and 10% were *M. armillata.* Among 11 flies collected along a small stream near Atenas, 73% were *M. mitis*, 9% were *A. discolor*, and 9% were *A. armata.* Scattered flies were so dispersed that there were no interactions.

Males in aggregations generally outnumbered females. The mean percentage of males in 517 flies sampled from six aggregations was 60 ± 7% (assuming, conservatively, that all females were *M. armillata*). Spatial heterogeneity in sex ratios within aggregations was suggested by samples from an aggregation in an overgrown coffee field: of 65 flies in the 30- to 50-cm-diameter central area of greatest concentration, 85% were males (91% of the males were *M. armillata,* and the rest *M. mitis*), whereas of 90 collected at the periphery only 43% were males (56% of these were *M. armillata* and the rest *M. mitis*) (differences between center and periphery in both sex ratio and in species of males were significant, respective chi-square values were 27.0 and 17.6, both df = 1 and $P < 0.001$).
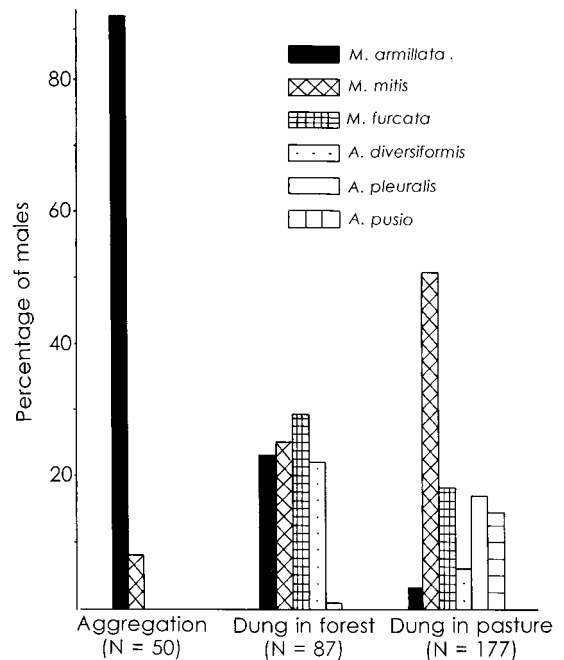

Fig. 1. Relative numbers of male sepsids collected at an aggregation near a small creek in secondary forest, at fresh cow dung (<1 h old) ≈10 m from the creek in the forest, and at fresh cow dung in a pasture ≈20 m further away from the creek. The relative abundances of all six species differed between the dung pats and the aggregation ($P < 0.01$ with χ^2).

Collections of flies drawn to fresh cow dung placed 10–20 m away from two different aggregations (one at a stream, the other away from water) revealed that the aggregations were far from a random sample of the species of sepsids present in the area. Comparing flies at dung in forest ≈20 m from an aggregation at the side of a stream, and at similar fresh dung ≈20 m farther away in an open pasture (Fig. 1), *M. armillata* were more abundant in the aggregation relative to males of the two other species of *Microsepsis* and three species of *Archisepsis* collected (chi-square values were 60.5 and 179, respectively, both df = 1, $P < 0.001$).

Those flies found in pairs in aggregations were all copulating; in no case was the male only riding the female as is common in other sepsids (Parker 1972a, 1972b; Schulz 1999) and in *M. armillata* on dung. Copulating pairs were relatively rare. In seven surveys at three different aggregations, only 0.38% of the flies were copulating (2,056 solitary flies, four pairs). More than 50 mounting attempts (all of which failed) were observed, and several hundred brief aggressive interactions in which one individual (probably a male) struck his head against another, briefly tangled side-to-side, or pursued the other fly to the edge of a leaf. One mating pair that was encountered by another individual (probably a male) was not attacked.

In total, 46 solitary and nine copulating females from four aggregations were dissected. Copulating females had less well-developed ovaries than solitary females.
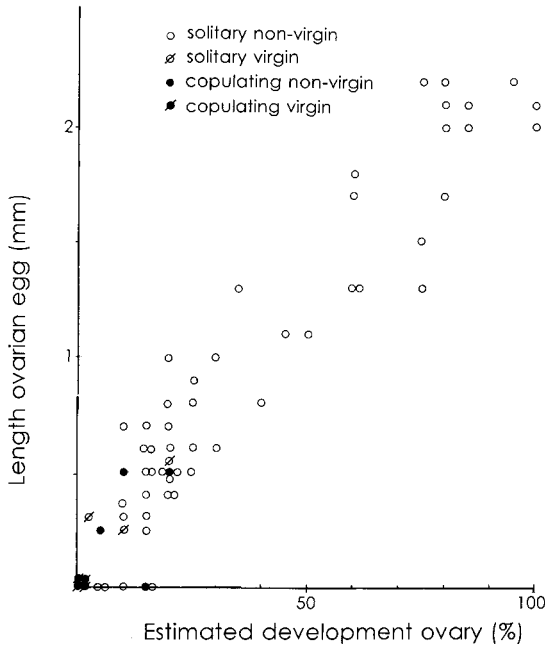
Fig. 2. Two estimates of the readiness to oviposit of virgin and nonvirgin females found in aggregations. Nonvirgins of all degrees of ovary development were present, whereas virgins all had relatively undeveloped ovaries.
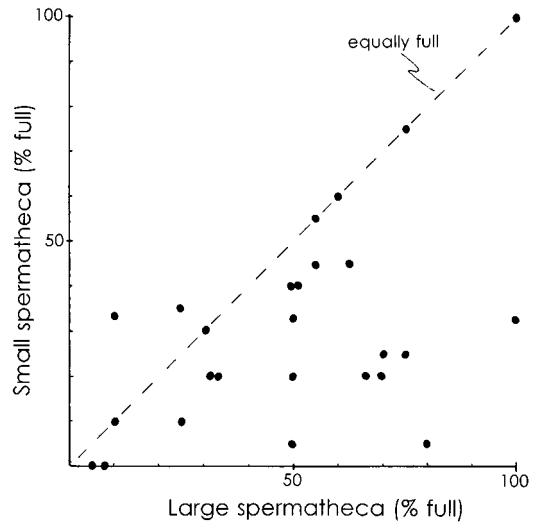

Fig. 3. Estimated degree of filling of large and small spermathecae in nonvirgin females. In all but two of 26 females both spermathecae had sperm; the large spermatheca was nearly always as full or more full compared with the small one.

All nine copulating females had ovaries that were 20% or less developed, and 55% of them were <10% developed; corresponding numbers for solitary females were 30.4% with ovaries ≤20% developed, and 10.9% <10% developed (both *P* < 0.0004 with Fisher exact tests) (Fig. 2). Copulating females were also more likely to be virgins than were solitary females (5 of 9 versus 2 of 46, *P* = 0.01 with Fisher exact test). The spermathecae of the four nonvirgin copulating females were about half to two-thirds full of sperm. Copulating virgins had little ovary development (0–2%). Solitary virgins also had relatively undeveloped ovaries (two were <5% one was 20%). The large spermatheca, whose duct is longer from the point where it branches from the basal, common spermathecal duct, consistently had larger absolute masses of sperm, and was also usually relatively more full of sperm than the small spermatheca (Fig. 3).

In 28.3% of the solitary females the bursa was not empty. It contained a mature egg (five individuals), a larva just hatched from the egg (three individuals), or a spermatophore (four individuals). Each of these females had sperm in her spermathecae. Those with spermatophores all had relatively undeveloped ovaries (all <20%), whereas those with eggs or larvae all had relatively well-developed ovaries (all ≥60%). In all but one female the egg in the bursa was clearly larger than any of the eggs in the ovaries.

Nine additional females copulating near fresh dung were dissected. Their reproductive and intestinal tracts were quite uniform. All had sperm in at least one spermatheca, moderately developed ovaries (10–30%)

with only small apparent eggs (0–0.7 mm), and full mid-intestines containing dark green-brown material (probably freshly consumed dung). Their crops were from one-quarter to completely full of clear, transparent liquid. The clear contents of the crop were presumably nectar or other liquid that was appreciably more viscous than the saline solution; when the crop was broken, the contents flowed slowly out and fell to the bottom of the dissection dish and gradually diffused away.

Two females copulating in an aggregation had no appreciable material in their intestines (the same was true for one virgin *M. mitis* female), and another virgin female collected while copulating had a midintestine full of dung. All virgin female *M. armillata* (both copulating and solitary) had clear liquid in their crops. The same was true for two noncopulating virgin *A. armata* females and five *M. mitis* females collected away from oviposition substrates.

Discussion

Female Feeding and Reproductive Biology. These observations support the speculation, based on less direct data from *S. neocynipsea*, that virgin female sepsids sometimes copulate at sites not associated with oviposition (Eberhard 1999). This interpretation is open to the objection that dissected females that had completely exhausted their sperm supplies or had emptied their spermathecae during copulation were misclassified as virgins. However, the consistent association of empty spermathecae and very small ovaries (Fig. 2) suggests that the females classified as virgins were indeed virgins. The same association occurred in five probable virgin *M. mitis* females and two *A. armata*

females that were collected away from oviposition substrates. It appears that in nature female *M. armillata* copulate long before they are ready to oviposit, as indicated by the lack of empty spermathecae among females that had at least partially developed ovaries. The contents of the digestive tracts of young virgin females suggest that they usually feed on nectar or some other clear liquid, and occasionally on dung before mating.

Nonvirgin female *M. armillata* also sometimes copulate away from oviposition sites, even though nonvirgin females follow the common sepsid practice of copulating at oviposition sites after laying their eggs. Thus, both the site and the timing of copulations varies in *M. armillata.* This sort of variation could help explain the variation in male escorting behavior and differences in the degree of sexual dimorphism that occur intra- and interspecifically in *Sepsis* (Schulz 1999). Other possibly important factors include differences in the intensity of competition among males on the oviposition substrate (Schulz 1999) and at other sites, and differences in the female's tendency to accept male mounting and copulation while on the dung as opposed to while she is on nearby plants after copulation is finished.

Maintaining a mature egg or recently hatched larva in the bursa has never been noted before in sepsids, and raises new questions regarding female receptivity to copulation. A mature egg has also been found in the bursa in females of both *M. mitis* and *A. diversiformis* collected away from oviposition sites (unpublished data). Both eggs and larvae, as well as the spermatophores that also occasionally occurred in the bursa of female *M. armillata*, would prevent intromission by a male, because the morphology of copulation in this species is very similar to that in *Archisepsis* (Eberhard and Huber 1998; unpublished data). Use of these objects as plugs to prevent intromission would seem superfluous, however, because females of *M. armillata* also resemble *Archisepsis* in apparently being immune to rape, because the proctiger of the female must be deflected dorsally by the female before intromission can occur (unpublished data).

The fact that some females had a young larva in the vagina indicates that the egg had been retained there long enough for the larva to hatch. The minimum length of time the egg must have been held in the bursa is suggested by the hatching times in other species, which vary from ≈6 h in *S. impunctata* at relatively high temperatures (Hafez 1939) to ≈1 d for *S. cynipsea* (Schulz 1989).The significance of the fact that all seven females of *M. armillata* with a mature egg or larva in the vagina also had relatively mature eggs in their ovaries (60–95% developed) is unclear.

Three possible explanations for how a mature egg came to be retained in the bursa occur to me. One comes from the observation of a female *M. eberhardi* Ozerov that had a single mature egg left in her ovary when she was collected while mating near dung. If, after the spermatophore that the male deposited was eliminated, presumably by the female digesting it as in *A. diversiformis* (L. Rodriguez, personal communica-

tion), she could have moved this egg into her bursa. A second possibility is that after oviposition the female matured a single egg more rapidly than all other eggs in her ovaries. This idea is not in accord, however, with the fact that no females were found with a single egg maturing more rapidly than the rest of the eggs in the ovaries. Perhaps the most likely possibility is that some females do not mate immediately after oviposition, but instead induce the male to dismount (as commonly observed in some *Microsepsis* and *Archisepsis* species) and then leave the oviposition substrate (as often occurs in some other sepsids; Parker 1972a, 1972b; Ward 1983; Schulz 1999) with a single unlaid egg, which is then moved into the bursa where it is fertilized and retained. Hatched larvae have been found in the bursae of many other groups of normally oviparous flies (Meier et al. 1999).

The data in Fig. 3 have implications regarding the functional significance of having two spermathecae, but further studies will be needed to determine whether the sperm in the two spermathecae have different probabilities of being used for fertilizing eggs. Such differential sperm usage occurs in both *Scathophaga stercoraria* (Ward 1993) and, comparing the seminal receptacle with the spermathecae, in *Drosophila melanogaster* (Fowler 1973).

Aggregations. The aggregations described here do not appear to correspond to the huge groups of *Sepsis* described by Pont (1979, 1987). Those of *Sepsis* differ in that they contain up to 100,000 flies, are much denser and have more sharply defined edges, never include mating pairs, sometimes include "frenetically active" flies, contain females that are all apparently virgins and nulliparous, and are not associated with food or water. Most of the aggregations of *M. armillata* probably resulted, in contrast, from the flies being attracted to food or water (during the dry season). Probably the flies, after feeding or drinking, spent time in the general vicinity, perched on leaves or other objects within 50–100 cm, as is common in many sepsids near dung pats and carrion. If this interpretation is correct, the striking lack of individuals of the other species present in the same immediate vicinity of *M. armillata* aggregations (two other species of *Microsepsis*, three species of *Archisepsis*) indicates that these other species must feed on as yet undetermined resources other than the rotting fruit and flowers of *S. obovata.* It may be significant in this context that *S. obovata* is strongly poisonous (Pittier 1978).

Because it was not possible to identify females to species, the quantification of biases toward males in the aggregations of *M. armillata* is only tentative. Nevertheless, the larger numbers of males, the frequent male-male aggressive interactions and mounting of females that occurred in aggregations, and the occasional presence of copulating pairs suggest that mating at such sites is frequent enough to play a significant role in the sexual biology of this species. An additional conclusion is that because sex ratios of flies raised in captivity were, if anything, biased toward females (62.9% of 70 flies in one clutch) (unpublished data), the apparent bias toward males in aggregations implies

that females must spend more of their time at still undetermined sites. The lack of recognizable dung in the midintestines of females collected at aggregations and at scattered resting sites, when combined with the observation that females at dung consistently had midintestines full of dung, suggests that females rarely move directly from dung to aggregations or solitary resting sites. In contrast, the tendency to find crops of even young virgin females at aggregations filled with clear, viscous liquid indicates that they commonly feed on liquids, presumably from decaying fruit and roots or perhaps flowers or other plant parts. Blanckenhorn et al. (1999) noted that individuals of *S. cynipsea* in captivity need sugar to survive, and speculate that they forage for nectar in the field. Females at all stages of their reproductive cycles occurred in aggregations, including young virgins, individuals with mature eggs that were probably about to oviposit, and females that had probably just oviposited and had large but empty ovaries.

Limitations of the Data. The survey techniques used may be biased toward one sex or the other if the behavior of males and females differs in ways that bias their chances of being observed or captured. Males are probably more active, and more likely to rest on the upper surfaces of larger leaves, rather than on the ground or smaller leaves, making them more easily sighted. Possible doubts regarding classification of females as virgins were discussed above.

Acknowledgments

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