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Mating Systems of Sepsid Flies and Sexual Behavior Away from Oviposition Sites by Sepsis neocynipsea (Diptera: Sepsidae)

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ABSTRACT: Females of several sepsid flies usually mate at oviposition sites only after having emptied their ovaries of eggs, leaving unexplained how the first batch of eggs is fertilized. Repeated mating attempts at a feeding site of female *Sepsis neocynipsea* suggest that copulations also occur at such sites, where sepsid behavior has seldom been observed.

Sepsid flies are characterized by an unusual mating system that, to date, has featured a "missing link". Males have been observed to wait near oviposition sites (almost always dung or carrion—e.g. Parker, 1972a and b; Mangan, 1976), mount and ride on females during oviposition and then mate with them. Parker (1972a) found that each of 56 females of *S. cynipsea* first seen ovipositing while carrying a mounted male copulated after having apparently finished oviposition. Copulations that could have fertilized the female's first laid eggs were not observed.

Dissections of female A. diversiformis (Ozerov) collected while they were engaged in different activities around cow dung near San Antonio de Escazu, San Jose Province, Costa Rica suggest a similarly strange, though perhaps slightly different mating system. The ovaries of 14 females that had just arrived at a newly produced dungpat and had not yet been mounted by a male contained a mean of 94 ± 19 eggs (range 44-126), while those of 23 females being ridden by a male as they walked over the surface of the dung contained fewer eggs (mean = 54 ± 40 , range 1-180) (p = 0.00094 with Mann-Whitney U Test). And of 35 females collected as they copulated on or near the dung, none had a single mature egg. In three of these latter females, however, the ovaries were relatively small, suggesting that the female had not produced or oviposited any eggs before copulating. In one female the ovaries contained relatively small eggs that were only partially mature. Since clutches of eggs appear to mature synchronously in this species, this female had probably also not oviposited mature eggs just prior to copulating.

Less complete observations of other species at this same site (and near Federal, Entre Rios Province, Argentina for *A. ecalcarata*) suggest similar mating systems. No mature eggs were present in the ovaries of 7 *A. ecalcarata* (Thompson), 9 *A. pleurulis* (Coquillett), 16 *A. pusio* (Schiner), 5 *A. discolor* (Bigot), 4 *Microsepsis furcata* (Melander and Spryer), and 1 *M. armillata* (Melander and Spryer) females collected while copulating near dung or carrion. Of these females, the ovaries were relatively small in one female each of *A. ecalcarata*, *A. pleuralis*, and *A. pusio*, and had many relatively small, partially developed eggs in one female of *A. discolor*.

Thus copulation by female sepsids often occurs soon after the female has laid all of the mature eggs in her ovaries. Possibly the reason females at oviposition sites refrain from copulating earlier is that the male's spermatophore, which is deposited in the bursa (Eberhard and Huber, in press), would block the exit of eggs from the female's reproductive tract (Eberhard, 1996). Unless females live long enough to produce about 10 clutches of eggs, which seems highly unlikely given their relatively short lifespan in captivity (W. Eberhard, unpub.), the infrequency of mating with females that have small, undeveloped ovaries leaves unanswered the question of where the matings occur that precede a female's first visit to an oviposition site and that are responsible for fertilizating her first batch of eggs (Pont, 1979).

Adult sepsids have been collected away from dung and carrion, on flowers and sometimes on other parts of plants (e.g. Pont, 1979). They probably feed away from dung, as it appears that a sugar meal is necessary soon after the adult emerges from the puparium: new adults of *Archisepsis* spp. and *Microsepsis* spp. raised in captivity consistently die if provided with only fresh dung, but survive well if given both dung and honey (W. Eberhard, unpub.). Nevertheless, sexual behavior has never been observed away from an oviposition site, though Pont (1979) intimates that it may occasionally occur in the dense swarms of

hundreds of thousands of *S. fulgens* occasionally found on vegetation. The observations of *S. neocynipsea* reported below offer a possible answer to the mystery of the missing matings.

Flies were observed on bushes of two currant or gooseberry (*Ribes* sp.) plants (close to *R. inebrians* and *R. cereum*) less than 1–2 m below the crest of Porter Mountain (el. 2200 m) near Lakeside, Navajo County, AZ on 8 and 9 July, 1998. Both bushes had some mature and immature fruit, but lacked flowers. The plant was identified using the field guide of Epple (1995). Determination of the sexes of flies in the field that were not collected was based on the degree of swelling of the abdomen (I have found that usually the abdomen of male *Archisepasis* spp. is recognizably thinner than that of nonspecific females).

At least five sightings of *S. neocynipsea* flies occurred on 8 July, and 27 more on 9 July. Of the flies sighted, 24 were males (the sex of 5 flies was confirmed by collecting them), and one was a female (sex also confirmed by collection), in 7 other cases I was uncertain of the sex. Nearly all flies walked actively over the leaves and occasionally the stem of the plant. Over the space of a few min each fly usually walked more or less continually, but stayed in an area 4–5 cm in diameter, only gradually moving farther away. I saw three brief aggressive interdictions in which one male lunged at or chased another. There were also six attempted mountings in which a male darted toward another fly from up to 2–3 cm away, generally after orienting toward the other fly from another leaf. The mounting fly climbed onto the other fly, but quickly dismounted, usually after the other fly wobbled its body vigorously from side to side.

The aggressive interactions, the male's tendencies to move frequently but not to wander widely, and the mounting attempts were all indistinguishable from similar behavior patterns of male *Archisepsis diversiformis*, *A. ecalcarata*, and *A. pusio* on and near cow dung (W. Eberhard, in prep.). As also occurs in these other species, males of *S. neocynipsea* did not defend consistently delimited territories, but rather attempted to mount or drive off other males in their immediately vicinity as they moved about.

One fly, a virgin female with well developed ovaries full of nearly mature eggs (confirmed by collection and dissection), was exceptional in that she moved more slowly and paused frequently to extend her mouthparts to touch the upper surfaces of leaves. The leaves were slightly sticky to the touch (as is typical of these species—Epple, 1995), so it seems likely that she was feeding. This female resisted a mounting male by vigorously wobbling her body.

At least seven additional flies were seen in the vicinity of about 1 hr old human dung about 100 m down the mountain in open forest of ponderosa pine (*Pinus ponderosa*) and pinyon pine (*Pinus sp.*). Five of the six flies that were collected were males. The female had few sperm in her spermatheca, and only partially developed eggs. No ovipositions were observed. One aggressive interaction and one mounting attempt (that failed) occurred near the dung.

These observations show that there are at least two types of sites where mating attempts occur in *S. neo-cynipsea*. Both are associated with resources utilized by females. The missing matings in other sepsid species may thus occur at female feeding sites, where the flies' behavior has very seldom been observed.

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