
Short Communication

Unusual Female-Aggregated Mating Systems in Phorid Flies

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Male Diptera often form mating/courting aggregations. Swarms of Nematocera and leks of Tephritidae are familiar examples (Sullivan, 1981; Sivinski and Burk, 1987). Female aggregations are much less common, and many of these are apparently not mating aggregations but simple accumulations at oviposition or foraging sites (see Sullivan, 1981). Among the Phoridae, typical male swarms occur in species of *Phora* and perhaps in a few *Megaselia* (Colyer, 1954). Autumnal indoor "swarms" of females may be no more than sheltering congregations of overwintering females. Other reports of large numbers of females can be ascribed to mass emergences or collections at oviposition sites; e.g., females of the parasitoid *Phalacrotophora herolinenis* Schmitz that gather on tree trunks may be attracted by the presence of their coccinellid hosts (Colyer, 1952, 1954).

The following describes female aggregations in *Megaselia aurea* (Aldrich) that appear to have a sexual function. Visiting males obtained mates from these groups whose members were not observed to feed, were unlikely to be freshly eclosed, and were often physiologically incapable of egg laying. Both all-female and all-male clumps were noted in a second phorid, *Rhyncophoromyia conica* (Malloch).

Observations were made during November, December, and January in an understory stand of palmetto [*Sabal minor* (Jacq.) Pers.] and deciduous saplings on the floodplain of Lake Alice, Alachua County, Florida. The site was ca. 86 m in circumference and it contained 55 palmettos (331 fronds) and 53 saplings,

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12 of which were cherry [*Prunus caroliniana* (Mill.) Ait.]. During warm weather (ca. 18°C and above) *M. aurea* were observed on 18 days and *R. conica* on 20 days. When the former was found, a numbered piece of tape was attached to the plant 30–60 cm from the actual occupied spot. A sapling of *P. caroliniana* occupied continuously by *R. conica* was replaced in January with a similarly sized sapling of laurel oak (*Quercus laurifolia* Michx.) and a palmetto frond. These cuttings were kept fresh by placing the cut end in a buried cup of water.

Megaselia aurea. Females were found singly and in groups on the upper surface of oak, cherry, and hickory leaves and, particularly, on palmetto fronds. Fifty-one observations of 125 flies were recorded from 19 leaves on 18 of the 108 similar plants in the site (mean females per group, 2.5; s, 2.3; range, 1–11 females per group). Twelve of the groups (24%) and 34% of all flies found were on a single palmetto frond (mean group size, 3.7; s, 3.3). The four most occupied leaves bore 26 (51%) of the observations and 56% of the flies. Six males were noted, only one of which was on a leaf where no females were present.

Females often scurried in circles several centimeters in diameter. Brief interactions that consisted of approaching to within a few millimeters of another individual followed by a rapid change in direction were common. When several flies simultaneously approached another, the group would assume a restless, milling, circular pattern. Stationary individuals stood within 1 to 15 cm of each other. The group composition was fluid, with the number of flies sometimes changing rapidly. Flights from the group appeared to be both spontaneous and the result of contact with another fly.

Three couplings were observed. Males swooped down and immediately mounted females. The pair would then instantly take flight. The entire process took about 1 s. The only observed courtship occurred when a male landed in the midst of a very tightly packed group of three females. The male appeared disoriented for an instant, scurrying in several directions before standing on extended legs directly behind one of the females and buzzing his wings. The moment he mounted, the pair took flight. The wing buzzing resembled the acoustic courtship display of the tephritid *Toxotrypana curvicauda* Gerstäcker and, likewise, may have been a sound signal (see Sivinski and Webb, 1985). Mated pairs apparently rest on foliage after they leave the original site. A single coupled pair was found sitting on the upper surface of an oak leaf. One male was seen to land within a few centimeters of a female clump and then leave after a second.

There was little to distinguish attractive (occupied) from unattractive (unoccupied) foliage. In the case of palmetto, occupied leaves tended to be horizontal, but they were not in consistently shaded or illuminated locations. Flies could be found on both sunny and overcast days. Interestingly, the same leaves

occupied by phorids also were used for very different sexual behaviors by other flies. Two tanypodin chironomid species formed typical male swarms of 10–30 individuals about 30 cm over palmetto fronds. Of the 11 swarms observed, 9 occurred over *M. aurea* sites. In several cases the two species were present simultaneously. Males of the tiny dolichopodid *Chrysotus pallipes* Loew kept apparent palmetto frond territories (repeatedly disturbed individuals would return to leaves up to four times), on which they would emit bright silver flashes from their enlarged and shiny palpi. All of the five individuals were discovered on sites that had at one time been or would be occupied by *M. aurea*.

Rhyncophoromyia conica. This fly was found at a single spot, which was occupied on every warm observation day from 2 December 1986 through the end of observations on 16 January 1987. The original sighting was on the top leaf of a cherry laurel sapling (ca. 1 m tall). A *M. aurea* had been taken from a leaf and when I returned a few minutes later with the marking tag, five female *R. conica* occupied the same leaf. The next day the tree was cut down by a vandal who left a 30-cm stub from which grew four leaves, one of which was damaged badly. Approximately 170 flies (range of 2–15) were seen on these few leaves over the next 18 observation periods (Fig. 1). The stump was then removed. A substitute branch was erected in a buried cup of water, while the original plant was put in a second buried cup 30 cm away. The first replacement

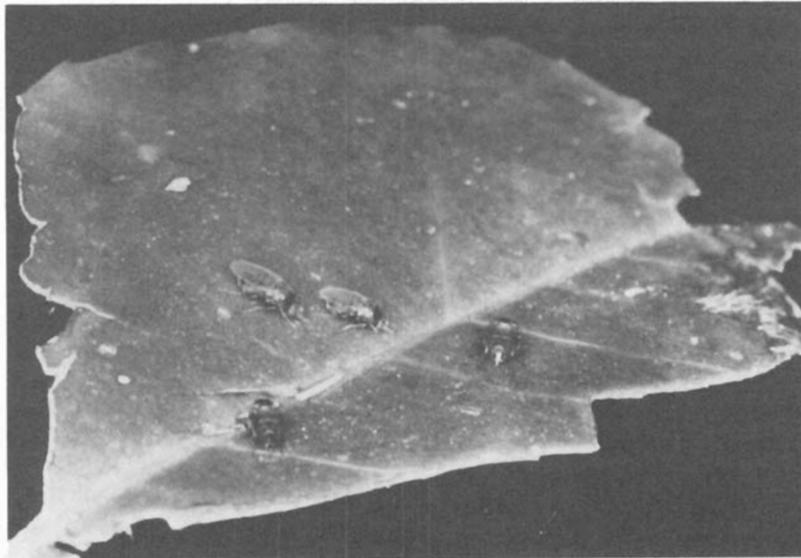


Fig. 1. *Rhyncophoromyia conica* on the favorite (most occupied) leaf of their "swarming" site; insects are ca. 1.5 mm long.

was a single laurel oak leaf. On the next warm day it bore six flies and the original leaf had none. This was replaced by a palmetto frond cut to a single ribbon ca. 15 cm long. The following day 15 flies were on or flying above it and there were none on the original cherry. Apparently, it was the location rather than some quality of the leaf or its previous occupancy that made this a suitable aggregation spot. This is all the more remarkable when one considers that most of the original sapling was removed, so that a site's height apparently is not one of its important features. There were two other cherry saplings within 2 m, 12 altogether, and 53 deciduous trees between 15 cm and 3 m tall in the site. *R. conica* was not found on any of these.

R. conica is very active, running, investigating other individuals, and taking short flights, so that a large proportion of the flies was a few centimeters above the leaves at any one time. Mating was similar to that of *M. aurea*, but even more difficult to observe. Males would rocket down and a coupled pair would appear to rebound from the leaf.

As in *M. aurea*, there are apparently all-female clumps of *R. conica*, but the lack of dramatic sexual dimorphism makes determining sex difficult except among netted individuals. Captured flies on different days tended to be all of one sex (5, 3, 10, 10 ♀ ♀; 5, 3, 2, 5, 6 ♂ ♂). There was only a single sweep that took both sexes (3 ♀ ♀; 4 ♂ ♂).

These unusual mating systems raise two questions. Why are female flies clumping? Why do they clump repeatedly on the same bits of foliage? It is unlikely that aggregation spots were either oviposition, feeding, or eclosion sites that concentrated females and which were then visited by mate-searching males. Of 8 dissected *M. aurea*, 7 had undeveloped ovarioles, as did 5 of 10 *R. conica*, making it improbable that they were searching for oviposition opportunities. *M. aurea* has been reared from a dead army ant and is probably a saprophage, while *R. conica* appears, from the structure of the ovipositor, to be a parasitoid (B. V. Brown, personal communication). In neither case was there an obvious resource at clumping sites that would hold numbers of flies in precise locations for long periods of time. As for feeding, there was no obvious food source on clumping sites and flies were not observed to eat (although small body size makes "negative observations" tenuous). Three of the dissected female *M. aurea* had guts distended with brown material; the others were empty. While female flies often feed more than males on sometimes different foods, the general absence of male *M. aurea* from the clumping sites is not particularly supportive of their being feeding sites, nor is the occupation of fresh leaves introduced into the *R. conica* site. It seems unlikely that three very different bits of foliage would rapidly accumulate a food resource found nowhere else in the area. As for clumping locations being resting and drying spots near eclosion sites, the developed eggs of several females and the full guts of three *M. aurea* are evidence of prior adult activity. The rapid movements, fluid form and com-

position of groups, and absence of males in *M. aurea* clumps further argue that these aggregates did not consist of sibling flies simply emerging from a common pupation location. On the other hand, the use of *M. aurea* aggregation spots for sexual behaviors in swarming chironomids and a territorial dolichopodid does suggest that these sites are unusually good ones for rendezvous or the broadcast of sexual signals. What signals these female phorids might emit, if any, are unknown. However, there is a striking color dimorphism in *M. aurea*. Females are yellowish orange with an iridescent orange patch on the dorsum of the abdomen that disappears upon death and drying. They are quite gaudy compared with the more nondescript colors typical of the family [see a colorful male in the possibly male-swarming species *Phora viridinota* Brues (Brues, 1916)]. Males are cream colored with dark dorsal areas on the abdomen and thorax, and I did not appreciate initially that the two sexes were conspecific. Perhaps the unusual female colors constitute a visual signal directed at potential mates.

Looking to the clumps themselves, their members give the impression of belonging to mating aggregations. Females pursue, catch, and then ignore each other as if they bear an initial interest in their neighbors and then become "disappointed." The immediate replacement of *M. aurea* by *R. conica* on the cherry sapling suggests that the presence of heterospecifics discourages aggregation. The instantaneous departures after coupling might even be interpreted as the female wishing to remove its smaller mate from the presence of potential rivals in the group.

Of these two remarkable mating systems, that of *R. conica* seems at first glance to be the more conventional, a variation of typical male aggregations. Both sexes were common at the site, if at different times, and the females clumping at some points and their absence at others might be due to the changing abundance of males. That is, when males, for some reason, are not present at their station, waiting females accumulate. If this is the case, then *R. conica* performs a very location-specific and extremely persistent form of male swarming. On the other hand, it seems just as likely that these few leaves could be a female aggregation site that males visit. By this argument, when arriving males are common, the female pool is exhausted quickly and only previously attracted males remain. This explanation emphasizes the possible similarities between the *R. conica* mating system and that of *M. aurea* with its consistently all-female clumps.

But what exactly is the role of female clumps in *M. aurea* and perhaps *R. conica*? There is insufficient information for an answer, but I mention several selective forces that might bring female phorids together. First, aggregations are incidental, an effect of relatively numerous females exploiting a few good, but very small, signaling sites. Second, females seek each other out in order to pool their displays on optimal sites and so enhance the range of their signals. In general, such cooperative signaling is unlikely to increase the area covered

per individual. However, under certain conditions, pheromones might be profitably pooled (Bradbury, 1981). Perhaps such a boost would be useful, particularly in little insects with a relatively small capacity for pheromone production. Third, some large male investment, perhaps in the ejaculate, has made access to males a limiting factor in female reproductive success, with a subsequent reversal in sex roles, i.e., brightly colored females displaying in a "lek" toward discriminating males [see Trivers, 1972; note the substantial ejaculatory investments in some flies such as certain *Drosophila* species (Markow and Ankey, 1984; Turner, 1986); see also the curious behavior of the female-swarming and nutpully-fed empidid *Rhamphomyia longicauda* Loew (Newkirk, 1970)].

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