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OBSERVATIONS ON SWARMS OF *RHAMPHOMYIA SOCIABILIS* (WILLISTON) (DIPTERA: EMPIDIDAE)

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Abstract.—The swarming behavior of *Rhamphomyia sociabilis* was studied at three neighboring sites in Larimer Co., Colorado. One swarm reformed at the same site for five years, another for four years; in each case the swarm formed in mid July and persisted for about a month. Males entered the swarm carrying prey and transferred the prey to females as the latter joined the swarm. Mating pairs moved about within the swarm and were not seen to settle. Prey consisted of small insects of six orders, about 70% of the prey consisting of Diptera.

Over the past five years I have had an opportunity to observe three swarms of *Rhamphomyia sociabilis* (Williston) (Diptera: Empididae) near my home 23 km west of Livermore, Larimer Co., Colorado, at 2,370 m elevation. Although the behavior of this species does not appear to differ in any important way from that of several other known species of the genus, few persons have had an opportunity to study swarming at one site over a full season or over a period of years. Although *R. sociabilis* was described from eastern Washington and is best known from the northwestern United States (Steyskal, 1984, and pers. comm.), it is evidently locally common on the eastern slopes of the Rocky Mountains in Colorado. In addition to the swarms described here, there is a long series in the collections of Colorado State University, collected in Evergreen, Jefferson Co., Colorado, by M. T. James (determined by James as *R. abdita* Coquillett, a synonym). Evergreen is ecologically similar to the locale of the present studies and is at about the same altitude.

STUDY AREA AND METHODS

Most observations were made at a swarm site along a path leading to my house (swarm I). The swarm moved back and forth in an aisle measuring 5 by 15 m among ponderosa pines and Douglas firs. The soil beneath consisted of fine gravel, of brownish color and largely devoid of litter and vegetation. Some 40 m to the southwest there was a rocky promontory overlooking a deep valley. Since summer winds are frequently from the southwest, the area is somewhat protected from these winds. This swarm site was discovered in 1983 and observed periodically through 1986; flies were absent from it in 1987. Successive generations of flies were obviously attracted to this site.

A second swarm site (II), about 300 m away, was studied briefly each year from 1983 to 1987, a five year span. Each year, the flies came to an aisle among conifers a short distance northeast of a rocky outcrop that overlooked this same valley. However, the soil here was largely covered with pine needles and clumps of short grass. A third swarm site (III), not discovered until 1986 but also active in 1987,

was about 7 km away but again among conifers northeast of a rocky prominence. In this instance the ground was mostly covered with fairly tall grasses and wild-flowers. All three sites were essentially dry, open forest; in no case were there streams or ponds within 0.5 km. Swarm sites II and III were used for making sweep samples from various parts of the swarm to obtain sex ratios and prey specimens, while swarm site I was used for observation and subject to minimal disturbance.

Shade temperature was recorded with a mercury thermometer and wind speed with a Dwyer wind meter. Observations were made against the sky, against a dark background of trees, or against a large sheet of black cardboard placed behind the swarm. At times, parts of the swarm were dusted with talc or with white flour and the time recorded until the last marked pair disappeared from the swarm.

Voucher specimens have been placed in the collections of the U.S. National Museum and of Colorado State University.

RESULTS

In 1983–1986 swarms at sites I and II varied from 6 to about 50 individuals, but in 1987 the swarm at site II increased to a maximum of about 120. The swarm at site III was very large both in 1986 and 1987, numbering several hundred individuals. Larger swarms produced a distinct, low humming sound.

In 1985 swarm I was seen to form in mid June and to have disappeared by mid July. More careful observations in 1986 revealed first swarming on 16 June and last (very reduced) swarming on 19 July. Between those dates a swarm formed for at least part of every day except 26 June and 18 July, days of nearly continuous rain. During 1987, swarm II was first noted on 19 June and was last seen on 19 July. Dates of study for swarm III were 4 and 15 July 1986 and 19 June and 3 July 1987. Evidently the flight periods of all three swarms were very similar.

During heavy showers the swarms tended to disappear, although a few flies often swarmed in a light rain. Wind gusts of 8–14 km/hr often caused the swarms to be slightly displaced and disorganized, but persistent winds of over 14 km/hr resulted in disappearance of the swarms. The flies were seen to start swarming as early as 0840 hrs (Mountain Daylight Time) and to remain as late as 2000 hrs, when the sun was very low on the horizon. Shade temperature appeared to have little effect on swarming; swarms were present as low as 16°C and as high as 29°C (these are very nearly the daylight extremes experienced at this altitude during the swarming period). In general, swarms seemed to prefer at least partial shade except in the early morning or late in the day, when they tended to drift into patches of sunlight. A thin cloud cover or passing clouds had no effect on swarming. On warm, clear days there was a noticeable decline in the size of the swarms at mid-day, and occasionally no flies were present at that time; little shade was available in the aisles between 1100 and 1400 hrs.

The swarms were by no means homogenous at all times. In fact three different subswarms could be detected. Most conspicuous was subswarm *a,* consisting of mating pairs with prey; these formed a compact cluster of slow-flying pairs, 2–3 m in diameter and 1–2 m high, though occasionally drifting upward to 3 m. Within this space individual pairs moved in irregular circles, figure 8s, and up and down movements, only 10–40 cm apart but rarely contacting one another. A second sub-

swarm (*b*) consisted mostly of males carrying prey; this was a more diffuse swarm, often 3–5 m in diameter, the males flying somewhat more rapidly than was the case with mating pairs. A third subswarm (*c*) always occurred laterally to and below the others; individuals (never with prey) moved back and forth so swiftly that they seemed no more than a streak. They moved in an elongate pattern 0.5 to 1 m above the ground. This subswarm consisted mainly of females.

Sweep samples confirmed the different sex ratios in these subswarms. The best samples were obtained on 4 July 1986 in swarm III. A sweep through subswarm *a* yielded 13 males, 13 females, and 13 prey. On this date the males formed their more diffuse subswarm (*b*) about 4 m away; a sweep through this subswarm yielded 20 males, 10 females, and a few prey. Adjacent to this subswarm was an elongate area beneath tree branches, about a meter high, filled with individuals flying very swiftly back and forth. A sweep sample in this subswarm (*c*) yielded 24 females and 6 males (no prey). Only a few of these females had distended abdomens, in contrast to those in subswarm *a*, in which many females had swollen abdomens (similar to those of mosquitoes that have just had a blood meal).

Only at the largest swarm (III) did I ever observe all three subswarms at one time. At swarms I and II it was common to see a diffuse group of prey-laden males (*b*) early in the morning and often, after a mid-day hiatus, in the early afternoon. The more compact subswarms of mating pairs (*a*) formed in mid or late morning and especially in late afternoon, and at these times the swift-flying individuals could often be seen forming an elongate pattern (subswarm *c*) nearby. Evidently males capture prey early in the day, and again later in the day, and fly together in a portion of the arena (subswarm *b*). As they are joined by females, they form a more compact subswarm (*a*) in which flight is noticeably slower. The swift-flying individuals in subswarm *c* are evidently mainly females that are about to join males or have just completed mating. Thus the pattern of swarm formation appears to be:

$$♀c \rightarrow ♂b \rightarrow ♀♂a$$

Observations on several species of this genus suggest that females are not predaceous, and the only food they take is that presented to them by males. Individual females evidently enter the swarm many times in the course of their lives, possibly several times per ovarian cycle (Downes, 1969). Although in the present case swarming occurred over a 30–32 day period, I have no information on the length of life of individuals or the number of times they enter the swarm. I never observed individuals of either sex, or mating pairs, resting on the ground or on vegetation, although I made an effort to find them.

It is difficult to observe the precise details of mating, but it is clear that males transfer the prey to the females soon after they make contact. Males are above the females, which feed on the prey during the aerial mating period. The wings of both partners are in motion during the mating period. I found it impossible to follow individual pairs for more than (in one case) four minutes. However, by dusting subswarm *a* with talc or flour I was able to watch the gradual disappearance of marked pairs up to 20 minutes, after which no marked pairs were present. That copulation of individual pairs is of much shorter duration than duration of the swarm is also suggested by the fact that up to one third of prey items taken in sweeps still showed movements of body parts; evidently these had only recently been transferred

Table 1. Families of insects taken as prey by *Rhamphomyia sociabilis,* with number of specimens taken.

Ephemeroptera	Hymenoptera	Milichiidae (3)
Baetidae, male (1)	Braconidae (4)	Otitidae (1)
Psocoptera	Formicidae, males (60)	Phoridae (17)
Myopsocidae (1)	Diptera	Pipunculidae (4)
Pseudocaeciliidae (1)	Agromyzidae (4)	Psilidae (3)
Hemiptera	Anthomyidae (35)	Scatopsidae (2)
Aphididae, alate (1)	Bombyliidae (4)	Scenopinidae (6)
Cicadellidae (18)	Cecidomyidae (1)	Sciaridae (16)
Delphacidae (1)	Chironomidae (13)	Sepsidae (6)
Miridae (15)	Chloropidae (23)	Simuliidae (17)
Psyillidae (5)	Dolichopodidae (13)	Sphaeroceridae (3)
Lepidoptera	Drosophilidae (2)	Stratiomyidae (6)
Psychidae (1)	Empididae (18)	Tachinidae (15)
	Ephydridae (4)	Tephritidae (1)
	Lauxaniidae (9)	Tipulidae (1)

to females. Other prey items in sweep samples were dead and in some cases shriveled and distorted. It is possible that some of these had been used a second time, as reported for a species of *Empis* by Hamm (1909).

Prey items varied considerably in size. Sixty-eight prey items, taken in swarm III on 4 July, varied in length from 2.0 to 4.5 mm (mean 3.3 mm). The longest prey I took from a swarm at any time was a male chironomid midge measuring 5 mm and thus about the same length as the empidid that carried it, though more slender. The bulkiest prey was a small moth with a body length of 3.5 mm and a wing length of 4.3 mm. Male ants were the most frequently taken type of prey, but they occurred only in swarm III, which was evidently near ant colonies. Diptera made up about 70% of the combined prey of the three swarms. It is interesting that although Empididae were used as prey fairly often, none of them were *Rhamphomyia sociabilis.* The list of prey (Table 1) is very similar to lists published for *R. scutellaris* Coquillett (Crane, 1961), for *R. curvipes* Coquillett (Powell, 1964), and for *R. longicauda* Loew (Steyskal, 1942, 1950; Newkirk, 1970). The 335 prey records represent 37 families of six orders. This compares with 20 families of four orders reported for *curvipes* and 29 families of six orders reported for *scutellaris. R. longicauda* is reported to use insects of six orders, with one record of a spider (Newkirk, 1970). In each case Diptera made up the majority of the prey.

DISCUSSION

The swarming behavior of *R. sociabilis* resembles closely that of *R. curvipes* as described by Powell (1964). The latter species, observed over a lawn adjacent to a hedge in Contra Costa Co., California, also showed a group of slow-flying, prey-bearing pairs and an adjacent subswarm of individuals (mainly females) flying very rapidly in elongate patterns; however, these flew higher than the mating pairs rather

than lower as in *sociabilis*. Most swarming was in the morning and late afternoon. Powell found the swarms at the same site in two successive years.

The observations of Crane (1961) on *R. scutellaris* extended over three years, the flies occurring each year over two sections of a trail near San Jose, California. He found that males bearing prey often alighted on bushes in the swarm area and that mated pairs left the swarm area, flying out of sight while still coupled. One pair remained in the swarm for 25 minutes before leaving. Alcock et al. (1979) found *R. pectoris* Coquillett swarming over pools of water and depressions in sandy roads on St. Catherine's Island, Georgia. Swarms formed in the evening on each of three days; at first they consisted of males, mostly with prey, but females soon joined and contacted the males. Copulation was apparently completed in flight. These authors surmised that non-prey-carrying males might intervene during prey transfer and usurp a female and prey from a competitor. I did not observe males without prey in swarms of *R. sociabilis*.

The behavior of *R. longicauda,* a species widespread in eastern North America, differs in certain particulars (Steyskal, 1941, 1942, 1950; Newkirk, 1970; also J. A. Downes and D. H. Funk, pers. comm.). In this species, swarms of females form at dusk in open places adjacent to vegetation or buildings. The females inflate their abdomens with air such that the pleural membranes are greatly stretched; the abdomen collapses upon being punctured. The legs, which are provided with series of scale-like setae as in many members of the genus, embrace the abdomen laterally (Steyskal, 1941, provides a sketch). The expanded abdomen and legs together apparently produce a large signal to which the males respond. This expansion of the abdomen is far greater than I have observed in *sociabilis* and probably not analogous to the distention I have interpreted as the result of engorgement. No unusual distention of the abdomen has been reported in *curvipes, scutellaris,* or *pectoris*.

It is clear that there is much variation within the genus. Downes (1970) presented a description of the swarming of *R. nigrita* Zetterstedt on Ellesmere Island, in northern Canada. This species swarms over markers such as piles of debris; mating is completed after the pair settles on a nearby object. Mating lasted 38 and 48 minutes in two observed cases. Another arctic species, *R. ursinella* Melander, is virtually non-flying and mating occurs on the ground. Downes (1970) discussed interspecific variation in several other species of the genus.

Chvála, in his review of swarming and mating in Empididae (1976) states that the sexes meet in the swarm but that mating pairs leave the swarm to complete copulation. I observed no mating pairs of *R. sociabilis* outside the swarm and gained the impression that females were leaving the swarm only after copulation was completed.

Although some species (such as *pectoris* and *nigrita*) respond to swarm markers on the ground, the situation in *sociabilis, scutellaris, curvipes,* and *longicauda* appears somewhat different. Each of these species reappeared each year at an arena consisting of a more or less uniform substrate flanked by vegetation and with an opening to the sky above. Crane (1961) states that he studied other parts of the trail where *scutellaris* was found, but discovered no other swarms. I explored other sites among conifers northeast of rocky promontories, seemingly very similar to sites occupied by *sociabilis* swarms, but without result. Yet there were differences in the three swarm sites, differences in ground cover and in the arrangement of trees (swarm II was in a shadier site than I, while III was in a more open site, with more widely spaced

trees). Yet these sites had certain features to which the flies responded (presumably visually) year after year.

As with most Empididae, the eyes of the male *R. sociabilis* are contiguous and are divided into an upper part with large facets and a lower part with small facets. In several species of Empididae it has been reported that the male approaches the female from below, then holds a position a few cm away and flies in unison with her before coupling (Downes, 1970). The enlarged facets of the upper part of the eyes are believed to play a role in this close maneuvering by the male. The lower facets (which are like those of the female) are evidently concerned with behavior common to both sexes (Downes, 1969; Chvála, 1976).

The legs of the females of *R. sociabilis* and several other species are fringed with large, scale-like setae, not present in males. Downes (1970) suggests that females may display to males before pairing. In *sociabilis* the legs of the female appear to hang downward, where they occasionally glitter in the light. In *longicauda* the legs are held laterally and enhance the breadth of the inflated abdomen. Frohne (1959) mentions an unidentified Alaskan species of *Rhamphomyia* in which the female is "garishly marked with an extensive silvery abdominal 'saddle' which flashes conspicuously as she crosses beams of sunlight." It seems very probable that females of several species of this genus do indeed display, behavior possibly permitting them to select from among the responding males one with a particularly attractive prey item.

It is interesting that males of *R. sociabilis* used Empididae as prey fairly frequently (Table 1) but were not found to use conspecifics. Cannibalism has, however, been reported in *R. scutellaris* (Crane, 1961) and in *Empis trigramma* (Hamm, 1933). In some species of *Rhamphomyia,* males do much of their hunting at swarms of other Diptera, such as mosquitoes (Downes, 1970, and his fig. 1). Considering the great diversity of prey taken by males of *sociabilis,* it seems likely that the males hunt over a wide area.

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