quent to the outbreak, 3,082 mosquitoes were collected (December 1957, January, April and May 1958) and processed in 62 pools, with no virus isolates.

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References


PREDATION OF DANCE FLIES (DIPTERA: EMPIDIDAE) UPON MOSQUITOES IN ALASKA, WITH ESPECIAL REFERENCE TO SWARMING

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Introduction. The purpose of this paper is to summarize observations of dance fly predators of mosquitoes and to invite attention of the mosquito worker to their interrelated swarming and mating habits. A skimmer dance fly seizes the mosquito during emergence of the latter from the pupa...emergence predation. I have read no earlier account than Séguy's (1925) succinct: "pendant une élosion d'adultes de Culicidés j'ai vu à Vincennes des Moustiques (Calico) non complètement dégagés de l'enveloppe nymphale, dont les téguments étaient encore mouss, saisir et dévorer par des Hilara qui volent en grand nombre à la surface de l'eau." Unaware of Séguy's observation I reported the same phenomenon for Aedes punctator by Rhamphomyia sp. as new (Frohne, 1952a). I first participated at this grim and silent tragedy beside a pond in a small clearing near Aulke Bay, southeastern Alaska while sweeping everywhere for a female Rhamphomyia whose mate was swarming with and preying upon male Aedes punctator. Such aerial predation at swarms, sharply distinguished from the aquatic predation at pools, was designated swarm predation (Frohne, 1952b). The following year Alexander Hubert (1953) reported another example of emergence predation upon two species of Aedes and a Culiceto from Montana by a Rhamphomyia tentatively identified R. (Megacytus) argenteus Bigot. The present narration is preliminary and impressionistic, and the dance fly predators, although all are abundant Alaskan insects, are virtually unknown to science.

None of the species of dance flies observed attacking Alaskan mosquitoes are yet designated specifically. I sent the Rhamphomyia predators of Aedes punctator to Dr. Willis Wirth of the U. S. National
Museum and received the following comment: "These species are probably new as I cannot identify them with any of Coquillett's or Malloch's Alaskan or arctic species in the Museum collection. There are hundreds of species to be described in this large and difficult genus" (letter, Alan Stone, 1952). Dr. Wirth advised appeal to Mr. G. E. Shewell of the Canadian Department of Agriculture, an empid specialist who has kindly indicated complexes without, however, assigning specific names. A representative comment of his (Shewell letter, 1955) explains: "I am sending you herewith a sort of report on your last shipment of empids. I am afraid that I cannot supply you with a single species name and this is not for want of trying... I hope that eventually I shall be able to give you names for them."

After 1952 I devoted a good many summer evenings near camp in various regions of Alaska observing dance flies swarming, skimming, hunting, or visiting flowers. My understanding of their behavior toward mosquitoes now rests on a broader basis although most of the observations have not concerned mosquitoes. In explaining relationships at joint swarms of the two families there is, of course, risk of inappropriate analogy. I have sought objectivity by accumulating specific details about the mosquito predators as well as by observing the other species which evidently ignore mosquitoes. My difficulties in the exercise of swarm-watching led to a sort of procedure. The observer must have time to repeat observations over and over and at different swarming sites. Each night sample collections of each swarm are put in separate, labeled killing tubes for examination next morning. It is scarcely worth while to accept aid of untrained helpers; swarm-watching is not for dilettantes. However, guests who arrive at swarm time are necessarily enlisted. When an evening must be skipped it may be worth while to give the swarm sites a look and a promise, if one returns before morning. Alaskan flies rarely swarm again at dawn, probably because it is usually too cold, but during the persistent twilight past midnight in June some activity may go on for hours after peak swarming. Weather and detailed estimations of aggregations and rates should precisely specify swarm location and time. General weather and average counts may mislead. The most useful data are repetitive records of individual swarms jotted down on the spot. For the weather it is best to record temperature, cloudiness, wind, rain, etc., when swarming begins and ceases, but this is not always practicable. Good comparative records (June) were made at 20:30 (Alaska Standard Time). More important than efficiency is leisure for revision and re-checking of impressions until a degree of predictability permits satisfactory conclusions.

Different dance flies characterize all sorts of habitats and microhabitats, especially the aquatic ones. For example, after heavy rain in McKinley Park in early July 1954, road rut puddles were covered over by flotillas, as it were, of scavenging skirmisher Hilara. In the spray of vertical, bridal veil falls near Juneau an especially large empid flitted or rested within the splash on the rock wall behind about middle of July. On July 7, 1953 notoriously stormy Naknek Lake was calm and I found it thinly covered by dispersed myriads of an empid skirmisher. The lake is forty miles long and several miles wide, yet a trip by outboard motor of over three hours revealed no break in this diffuse, countless host in ceaseless flight two or three feet apart, buzzing and striking at bits of flotsam. Among many such casual observations several additional examples of nexus between dance flies and mosquitoes were brought to light.

Swarm Predators. An Alaskan Rhamphomyia, resembling the one first reported preying upon Aedes punctor swarms at Auke Bay, attacked males of Aedes communis and catochyla observed in 1953 swarming in a glade near Chitina (Copper River valley) Alaska (Froline, 1954). The dance fly males, which usually greatly outnumbered the mosquito males they were seizing and carrying off, also swarmed on several evenings when no mosquitoes...
were seen at the swarm site. A few rare instances of mating of the *Rhamphomyia* at the swarm were spied and the female was then secured in *coitus*. Her wings are distinctively bicolored, partly clear, a condition evident in flight. If mating were the only purpose of the male swarms, the comparative rarity of females puzzled me, as it did in the species at Anise Bay the year before.

*Aedes excrucians* also swarmed at Chitina (Frohne, 1954). Dance flies ignored the *excrucians* swarms, which are rather spontaneous, large, diffuse aggregations with a loose core constantly moving irregularly about. Now and then the core dissipates and materializes unexpectedly like a djin of the Arabian Nights at another point twenty or thirty feet away. *Excrucians* did not swarm in the secluded glade chosen by the other two *Aedes* but instead over a spacious clearing not far away. Although this larger species has a very different swarming behavior from the furtive, rather persistent, definitely localized *communis* and *cataphylla*, I thought the erratic swarming habit of *excrucians* might afford the species a certain immunity from attack of glade-swarming dance flies, but the idea did not find support in the following season's observations.

The following June the identical *Rhamphomyia* was observed preying on swarms of *Aedes communis* peculiar to the arctic open-country focus of that species occurring in the relatively treeless taiga near timber line in Mt. McKinley National Park, Alaska (Frohne, 1955). The *Rhamphomyia* swarmed here quite in the open but against the cores of its swarms coincided with the cores of *communis* swarms. At times the dance fly males outnumbered the mosquito males and harried individual mosquitoes out of the common swarming site. There were several evenings when no male *communis* swarmed, but their absence did not discourage a large swarm of male *Rhamphomyia* from assembling. That summer excellent visibility conditions and ample time favored corollary observations, which provided some missing facts on the female with the bicolored wings. During lulls at swarms, roaming about searching for additional swarm sites, I found secluded swarms composed almost entirely of this bicolored female. Two such swarms were followed several nights during the last week of June. The sites were similarly sheltered by bushes adjacent to a bluff, situations rather like the glade swarming site of the male at Chitina. Unfortunately visibility was rather poor at female swarms. Predation was not seen but should not be ruled out altogether. No mosquitoes swarmed there. The most notable observation was that mating took place at frequent intervals, indeed, every time a male dance fly entered the swarm a scuffle ensued, and a pair left the swarm. I hoped to see instances of males bringing offerings of prey, especially of male *communis* which would have clarified the status of the male swarm of this *Rhamphomyia*, but no instance was seen. Contrasting activities seen at the two types of swarms, male and female, it appears the female swarm has assumed reproductive responsibility abandoned by the male. The whole question of female predation awaits further observations.

**Emergence Predators.** In the Katmai National Monument, Alaska Peninsula in 1953 I encountered a *Rhamphomyia* skimmer much like the Anise Bay skimmer of the previous summer. However, the new fly frequents streams rather than stagnant pools or ponds. As far as known it does not molest mosquitoes. Observation of its courtship and mating was nevertheless highly instructive and useful later on. The appropriate female was soon taken flying several feet above the stream while the males seldom left off skimming close over the water. This female is garishly marked with an extensive silvery abdominal "saddle" which flashes conspicuously as she crosses beams of sunlight in her gadding flight. Mating was repeatedly witnessed in broad daylight of mid-afternoon over a sheltered pool in a small, brushy stream at Kukak Bay. Copulation was occurring all afternoon from at least 15:00 to about 18:00 A.S.T., appearing always much the same: the
female flitted down flashing silver (as though taunting the skating males) several times; a male suddenly would lift from the surface, overtake her, clasp her; they would struggle momentarily, drop a foot or two, and then depart laterally into the alders fringe the pool. Evidently the female does not skim. This observation appears to confirm Hubert’s (1953) report from Montana that no females are taking skimming. It is not clear whether or not Hubert saw his species’ female but from the circumstances of its suggestive specific name, argentea, it is not unreasonable to suppose there may be a close relationship to the Kukak Bay species. At Auke Bay I had the impression that most of the drab females of that species of Rhamphomyia skimmer were otherwise and elsewhere occupied than with skimming, for I caught only a few of them sweeping over the water.

The following season, 1954, I encountered a pool skimmer at McKinley Park which does not differ, as far as I can see, from the Auke Bay pool skimmer. Because of the location of swarms of male Aedes communis under observation in a gravely, triangular wash enclosed by the confluence of Hines and Riley creeks, I followed the development of insects in some old residual oxbow pools in which large larvae of Aedes pullatus teemed from mid-June until the Fourth of July. Late in June the Rhamphomyia skimmer became abundant and though usually present in the daytime, too, its density increased and it skimmed more excitedly as the evening advanced. It was this build-up which led me to regard the skimming males as a swarm, an idea which is, I think, sound analogy. The peak of emergence for Aedes pullatus pupae at these pools came about July 1, and I then watched closely in the hope of discovering pullatus mating habits. Pullatus pupae are quite wary at emergence and usually seek shelter of the shoreline or a sprig of Equisetum, a floating stick, etc., to disclose the adult. The Rhamphomyia seized and ate up most of those emerging in the evening, however. I was rewarded one fine, early July night for staying until dark at the area by witnessing the mating of the drab skimmer. It was thanks to previous experience with the Kukak Bay flashy, silvery female that the observation was not missed. As it became almost too dark to distinguish the flies I watched their shadows against the reflection of the sky in the pool and noticed a remarkable difference in their behavior. Skimming tapered off more and more, and flies hovered two or three feet above the water. I guessed this might be a stage in the breakup of the skimming swarm, but I made a special collection and was delighted next morning to find my boxes mostly drab females. The following evening I saw quite well this swarm of females from a prone position on my back. Mating was taking place at a high rate until pitch dark, if not longer. Copulation was consummated away from the swarm as usual.

At McKinley Park in July 1954 and 1956 I also collected two species of empid skimmers of ponds belonging to Hilara. This is about as far as this observation goes; for neither kind was observed preying on mosquitoes. One of them is characteristic of alpine pools of a kind I have designated type VIII—cold, alpine pools fed by melt of adjacent snow-ice fields, Catla community (Frohne, 1957). It is to be expected that when this alpine Hilara is observed at times of emergence of Aedes pullatus or puncta its predatory habits will implicate it in the biologies of the mosquitoes. Aedes communis also breeds in these alpine pools but so early as to anticipate the flight period of the skimmer. The other Hilara skims permanent or temporary pools, even of rainwater, at elevations below timber line and is possibly a general predator, but nothing is known of its habits.

Discussion. The observations sketched seemed to indicate that mosquito predation by these empids constituted long-standing adaptations with evolutionary survival value. Predation, swarming and mating are rather mixed up, but they obviously occur regularly, and are not merely occasional, or incidents of exceptional occurrence.
Many more data are needed to interpret the significance of male swarms, especially those in which predation is an added complication. It is to be hoped that mosquito workers will become interested. Some speculations which need testing are: (1) The swarming male empids preying upon a male mosquito swarm are a sexual manifestation quite as much as the mosquito males; (2) Skimmer predators are likewise primarily a sexual swarm and females are as exceptional among skimmers as in other male swarms; (3) Predation is stimulated by presence of prey and light is a less important stimulus; (4) Stimuli for mating are more precise, and proper light conditions are prerequisite. If these impressions are confirmed, male empid swarms may be considered to subserve predation except at certain times when light conditions permit more or less mating. As mating becomes obsolescent in male swarms the female behavior becomes more and more swarm-like. Female swarms seem to be developing to take over the sexual function. In the male, predation has pirated the swarming habit. Evidently female dance flies, like many other Diptera, swarm relatively much less, only when copulation is imminent. The question of securing prey by the females should be investigated, for it is evidently quite different from the corresponding male predation, and is probably an individual enterprise independent of swarming. By analogy light may be shed on nonfunctional male swarms of mosquitoes by study of empid male predatory swarms.

**Summary.** Two types of empid predation upon Alaskan mosquitoes are distinguished. In one type, exemplified by an uncertain species of *Rhamphomyia* which attacks *Aedes punctator*, *communis*, and *cataphyllo*, *Rhamphomyia* males swarm in the evening in the identical swarm sites of the male mosquitoes. In a second type illustrated by a different *Rhamphomyia* sp., predation is upon *Aedes punctator*, *pionip*, and *pullatus* as they emerge from the pupae. This *Rhamphomyia* is a diurnal pond skimmer, but its skimming habit appears to be analogous (in a strict sense homologous) with swarming, because mating takes place in connection with skimming, and the species has, apparently, no other type of male swarm. Preliminary observations on similar habits of other Alaskan empids are reported.

**References**


