OBSERVATIONS ON MALE SWARMS OF *PSOROPHORA COLUMBIAE* IN TEXAS RICELANDS[1]

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ABSTRACT. The evening swarming behavior of newly emerged male *Psorophora columbiae* was studied in eastern Texas ricelands. Near infrared-sensitive video equipment was used to record swarming as it occurred in the field during each night of observation. Males of *Ps. columbiae* form either funnel-like or curtain-like marker swarms over a variety of objects in a riceland habitat. The seqence of events leading to swarm formation is described. Swarming males fly into the wind and follow a figure-8 pattern of flight. This flight pattern is modified by other insects flying through or near the swarm. Sudden changes in wind velocity or direction also modify the position and shape of the swarm relative to the marker over which it has formed.

INTRODUCTION

Psorophora columbiae (Dyar and Knab) is the most common floodwater mosquito species associated with riceland agroecosystems in the southern United States (Horsfall 1942, Olson and Newton 1973). Riceland areas provide a wide array of breeding habitats for *Ps. columbiae* (Schwardt 1939, Horsfall 1942, Meek and Olson 1976, Olson and Meek 1980); and the vast numbers of *Ps. columbiae* adults emanating from these agricultural wetland habitats pose a serious threat to the health and well-being of human and livestock populations.

Abatement of southern riceland populations of adult *Ps. columbiae* relies heavily on the aerial and ground dispensing of adulticidal chemicals after the adults have dispersed from their emergence sites. Participants in USDA, CSRS Southern Regional Project S-122 are proposing that a more effective and environmentally safer method of controlling *Ps. columbiae* in the adult stage would be to spot-treat newly emerged adult populations while they are still concentrated at their emergence sites. Such a strategy predicates a better understanding of the flight behavior of riceland populations of this species. In 1979 a 4-year study on the immediate post-emergence flight behavior of riceland populations of *Ps. columbiae* was initiated in Texas to provide such information that is basic to proposed control strategies.

The only earlier work dealing with *Ps. columbiae* flight and swarming behavior was that of Provost (1956) in Florida. Horsfall (1942) described the basic biology of *Ps. columbiae* in Arkansas ricelands, but did not describe or discuss the swarming or flight behavior of these populations in detail. The objective of the current study was to expand on Provost's (1956) information and relate it to *Ps. columbiae* populations occurring in the riceland areas of the southern U.S. Other publications on mosquito swarming and flight behavior referred to during this study and used in the interpretation of data included those by Charlwood and Jones (1979), Downes (1958, 1969), Edman et al. (1972), Frohne and Frohne (1952), Knab (1906), Nielsen and Haeger (1960), Nielsen and Nielsen (1953), Nielsen and Nielsen (1958, 1963), Nielsen and Nielsen (1962), Provost (1953, 1960) and Pausch and Provost (1965).

MATERIALS AND METHODS

The field sites used were located in the eastern Texas ricelands of Jefferson Co. (near Beaumont, TX) and Chambers Co. (near Anahuac, TX). Each study site was chosen on the basis of the presence of late instar larvae, pupae or newly emerged adults of *Ps. columbiae* in adjacent fields.

The propensity of many mosquitoes to swarm over objects that contrast to the background has been established (Downes 1958, Nielsen and Haeger 1962, Sullivan 1981). John B. Welch noted during his field studies near Anahuac, TX that *Ps. columbiae* populations in eastern Texas ricelands exhibited the same behavior.[4] This behavioral trait was exploited to cause male *Ps. columbiae* swarming at locations that were convenient for study. To accomplish this, a flat, dry area with uniform vegetation was selected as the point of observation at a given field site. A white flannel cloth (at least 2 m × 2 m) was spread as level and smoothly as possible over the ground at the observation point (Fig. 1A). The cloth served as the artificial marker

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over which swarms of male mosquitoes would eventually form. The swarms were then observed and recorded for further study in the laboratory using the equipment shown in Fig. 1 and described below.

Mosquito swarms forming over the cloth marker were viewed on the 21.5 cm (diag.) screen of a Hitachi®[5] black and white video monitor located on a card table positioned approximately 15 m from the marker site. The monitor was connected by cables to an RCA® TC2000 video camera positioned on a tripod next to and overlooking the area just above the flannel cloth (Fig. 1B). The camera was designed for night surveillance purposes by being equipped with a tube sensitive to visible light and having an extended sensitivity into the near infrared light region. Such a camera is capable of forming full video images at illumination levels of only 0.861 lux.

card table supporting the video monitor and was used to continuously record the mosquitoes swarming over the cloth marker. Recordings were taken at Beta® I speed (1-1½ hr recording time/cassette).

Since sound is believed to be of importance in mosquito behavior (Nielsen and Haeger 1960), a sensitive, directional microphone provided input to the sound track on the video-cassette tape. The microphone assembly used was a P650 parabolic microphone manufactured by Gelco Electronics®, Ltd. (Toronto, Ont., Canada). Sounds of mosquitoes swarming were recorded with the microphone placed on a tripod adjacent to the edge of the marking site (Fig. 1D). Output lines from the microphone were connected to the microphone jack on the VCR.

Because ambient light levels were too low for full video imaging during much of the swarm-

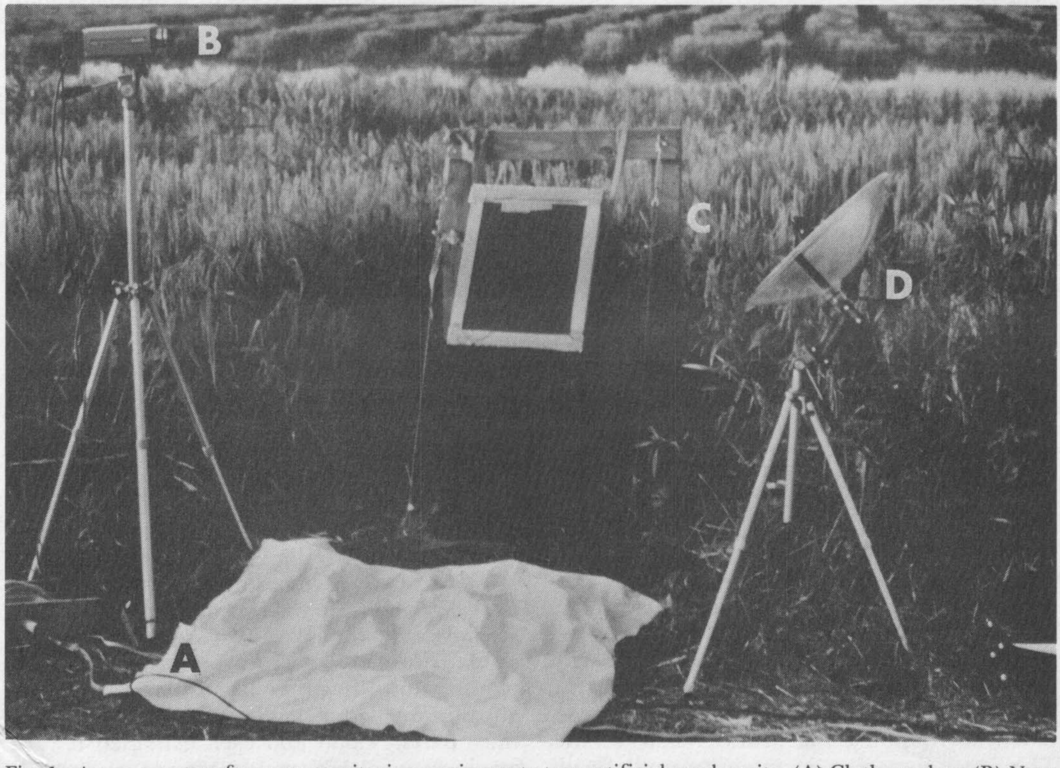

Fig. 1. Arrangement of swarm-monitoring equipment at an artificial marker site. (A) Cloth marker; (B) Near infrared-sensitive video camera; (C) Near infrared light source; (D) Microphone assembly.

Also connected by cables to the camera was an industrial Sony® Beta-max video-cassette-recorder (VCR). The VCR was located on the

ing period, an infrared light source illuminated the swarming mosquitoes (Fig. 1C). Mosquitoes do not respond to infrared light as they do to visible light (Clements 1963); thus, this illumination can be used to study mosquitoes in the dark without altering their behavior.

The video camera, VCR, monitor, mi-

[5] Mention of a commercial or proprietary product does not constitute endorsement by the USDA, TAES or Texas A&M University.

crophone and infrared light source all required 120v 60hz alternating current. This was supplied by a portable Dayton® Model 3W013C gasoline generator (Dayton Electric Manufacturing Co., Chicago, IL) that could provide 1.7 kw of electrical power. The generator was equipped with a 4-liter gas tank to extend the continuous running time of the generator to 4 hr which permitted all video recordings over a given swarming period to be made without refilling.

The generator was located about 50 m away from the swarming marker site to reduce any effect that noise and fumes might have on the swarming mosquitoes. Power was carried to the observation site by 2 flexible cables. The cable connecting to the video equipment was an 18-gauge, 3-conductor extension cord. The infrared light source required about 1 kw power; thus, its power cord was a heavier 14-gauge, 3-conductor cable. Both cables were insulated with rubber-like material for safety in wet or damp conditions.

Sweep net samples were periodically taken from the mosquito populations swarming over the marker cloth. These samples were used simply to verify identities of the insects seen in the video images and were not taken for purposes of obtaining quantitative data. Sweep net samples were taken from the surrounding vegetation as well. All sweep net samples and video/sound recordings were taken to the laboratory for further study and analysis.

RESULTS

Swarm formation observations. Swarming activity of male *Ps. columbiae* was observed both in the evening (after sunset) and in the early morning (before sunrise). The observations described here, however, will pertain only to the evening swarms since more observational data were recorded for these particular swarms.

The general sequence of events observed before and during the onset of evening swarming by male *Ps. columbiae* was as follows. Just after sunset, while there was still considerable light and before males actually began to swarm, mosquito flight noises were heard in the vegetation surrounding the artificial marker site. The noise increased in intensity until finally funnel-shaped swarms of male mosquitoes began to appear over the artificial marker and other marker sites in the vicinity. This series of events generally began about 20 to 45 min after civil sunset, and all evening swarming activity ended about 45 to 60 min later.

Video recordings made on the evening of June 15, 1982 documented the events surrounding the initial departure of mosquitoes from their daytime resting sites in the vegetation. On this evening, the video camera was aimed to the south immediately over the top of the vegetation in a rice field where male swarming had occurred the previous night. Sweep net samples taken before swarming activity began from vegetation next to the road where the video system was assembled verified the presence of both male and female *Ps. columbiae* adults in the area. The females included in the samples were later determined in the laboratory to be uninseminated. After sunset (2018 hr local time) and before swarming commenced, the characteristic flight noises of mosquitoes were heard in the vegetation. The intensity of these noises gradually increased; and at 2054 hr, the video system recorded a few mosquitoes rising up out of the vegetation from where the sounds emanated. The numbers of mosquitoes flying up increased over the next few seconds until suddenly, a large mass of mosquitoes (well in excess of a thousand individuals) arose at one time. This initial exodus (Provost 1960) was followed within the next 2 min by the rising of a second mass of mosquitoes. Within 6 min after the first mass exodus was recorded, a large, funnel-shaped swarm of male *Ps. columbiae* came down out of the sky and became positioned over the marker cloth. None of this flight activity could be seen directly by field observers at the time it was happening due to the low light levels. It was only by later reviewing video-recordings that the events surrounding the mass exodus of mosquitoes from the vegetation were detected and described. These recordings are on file at the Mosquito Research Laboratory at Texas A&M University.

The best observations of the manner in which male *Ps. columbiae* descend down over marker sites were made on the evening of August 15, 1982. Just before swarms began to form over markers on this evening, an observer sighted a layer or sheet of mosquitoes (ca. 1 m thick) hovering about 9 m above the ground. Within seconds after the layer of mosquitoes was first sighted, funnel-like proturberances began extending down from the layer. These protuberances resembled tornadoes dipping down from their parent cloud and each extended toward an object over which male mosquito swarms had formed on previous nights. Within a minute after these proturberances began to occur, the layer of mosquitoes dissolved and only funnel-shaped columns of mosquitoes could be seen swarming over various marker sites in the area.

The events just described were taken from voice recordings and field notes made by the person who first sighted the layer of mosquitoes. Fortuitous positioning of the mosquito layer between the observer and the western horizon where the sun had just set allowed for these observations to be made with the naked eye. Attempts to video record these particular events failed. All the events observed as leading to the formation of evening marker swarms by male *Ps. columbiae* in eastern Texas ricelands are summarized in Fig. 2.

Objects over which male *Ps. columbiae* evening marker swarms were actually observed during this study included shell roads, gravel shoulders of hard-surfaced roads, canals, puddles of water, low bushes, small trees, tree lines, dead trees, small stands of bunch grass, vehicles, the generator used in the study and people. Swarms probably occurred over other objects such as large trees, but they could not be seen owing to the low light conditions, small size of the insects and their distance from the observer. Sounds common to those associated with swarming male *Ps. columbiae* were heard on one occasion over a large tree next to a rice field near Stuttgart, AR during July 1981. Other swarms were observed in this region of Arkansas over the 4-year period of this study giving evidence that the observations made in Texas on male *Ps. columbiae* swarming behavior probably pertain to populations of this species occurring in other rice-producing areas of the southern United States.

SWARM MORPHOLOGY OBSERVATIONS. Two types of morphology were recorded for evening marker swarms of *Ps. columbiae* males observed in eastern Texas ricelands. The first type was that of a funnel (Fig. 2D). The tip of the funnel often occurred less than 1 to 3 m above a given marker. Funnel-shaped swarms were most commonly seen over objects that were small or at least not noticeably elongated.

The second type of marker swarm had the general appearance of a curtain. This type of swarm was most frequently observed over elongated, narrow objects such as roads, tree lines and, occasionally, over canals.

The vertical distance from the base to the top of *Ps. columbiae* marker swarms observed in eastern Texas was highly variable. Some swarms extended for just a few meters up into the air; others attained much greater heights. In the latter case, one hugh funnel-shaped swarm observed in Jefferson Co., TX during June 1982 was estimated, after reviewing videotapes taken of the swarm, to be over 70 m tall. The swarm was estimated to be about 0.5 km from the site where the video system had been set up and the full extent of the column was visible on the video monitor screen. Mr. John Steagall, a pilot for the Chambers County Mosquito Control District, supports this estimate by stating that he frequently has flown through swarms that were at least 61 m high. He further stated that he could see mosquitoes in the swarms as he passed through them with many mosquitoes striking the plane's

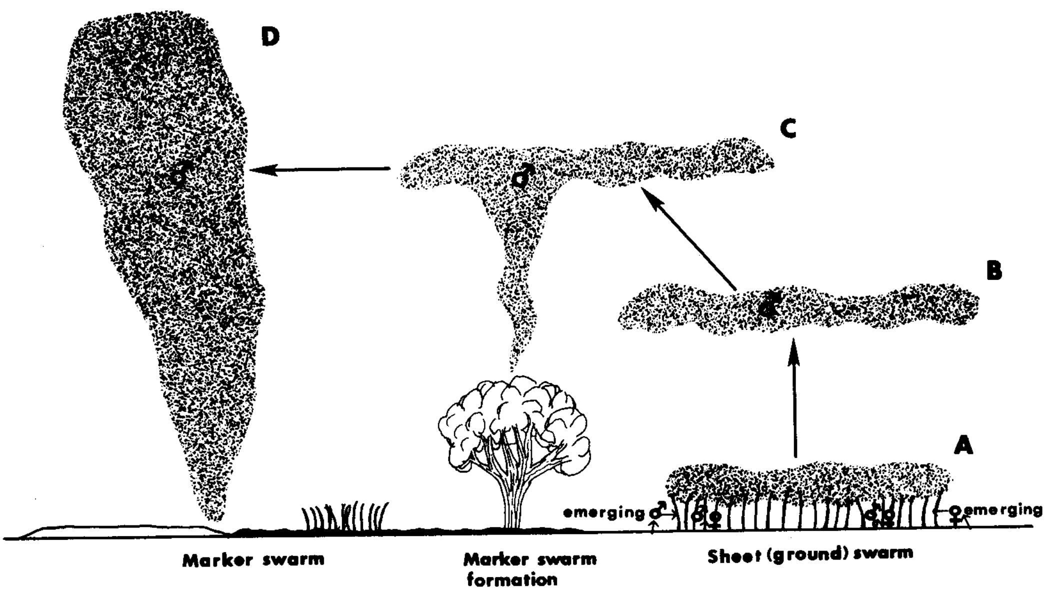

Fig. 2. Diagram of the events leading up to the formation of an evening marker swarm by *Psorophora columbiae* males in eastern Texas ricelands. (A) The *suspected* "ground-swarm" phase; (B) The observed layer-or sheet-swarm phase; (C) The observed column-formation phase; (D) The columnar swarm phase; (♂) males and (♀) females of *Psorophora columbiae*.

windshield. After the start of this investigation, Mr. Steagall's plane was examined on a few occasions after he reported passing through swarms at altitudes of 60 m or more. The examination revealed large numbers of dead male and female specimens of *Ps. columbiae* crushed on the leading edges of the wings and windshield of the aircraft.

Reduction in the size of the marker cloth did not appear to influence the general appearance of male *Ps. columbiae* swarms forming over the cloth. When the size of the marker cloth was reduced by folding it to ⅛ its original size, no observable change was seen in either the height of the mosquitoes in the swarm above the marker or in the number of mosquitoes comprising the swarm.

The vast majority (>99%) of mosquitoes occurring in sweep-net samples taken periodically from the swarms at ground level (i.e., no samples were taken any higher than approximately 3 m) were male *Ps. columbiae,* although a few females were collected on occasion. Specimens of other insect species, including other mosquito species, also occurred occasionally (<1% of the total specimens collected) in the sweep-net samples (Table 1).

Videotapes supported what was shown by the sweep-net samples in that they too indicated females of *Ps. columbiae* rarely associated with the male swarms, at least at levels below 3 m above the ground. Whether females may be interacting with swarming males more frequently at higher levels could not be determined during this study.

Flight behavior observations. Swarming males of *Ps. columbiae* flew over the center of the cloth markers used in this study. There was almost always a slight breeze (1.6–7.1 km/hr) during the observation period, and the males in the swarm invariably faced into the wind. When the wind speed increased, the swarming males moved slightly downwind and lost altitude and correspondingly, the vertical axis of the swarm tilted from nearly vertical (90°) to a smaller angle with the top of the swarm farther downwind than the bottom. At the same time, the bottom of the swarm usually remained centered over the marker or moved only slightly towards the downwind edge of the marker.

A review of videotapes centered on observing the flight activity of individual males comprising a given marker swarm indicated each male *Ps. columbiae* performed a figure-8 movement over the marker cloth while facing into the wind. The figure-8 path of flight was usually oriented vertically, although there was a horizontal aspect to this movement. Most of the time, the males would maintain a steady cruising speed in the swarm; but occasionally, they would speed up markedly. This would happen most often when other insects (some possibly female *Ps. columbiae*) passed by. It was also noted that swarming males increased their flight speeds in response to certain other sounds such as tone inflections of human voices.

DISCUSSION

Our observations confirm that *Ps. columbiae* males form marker swarms over a variety of objects in southern riceland systems. The general appearance of these swarms is similar to the descriptions of Provost (1956) for this species in Florida. Marker swarms of *Ps. columbiae* males observed in our study resembled the general nematoceran swarm described by Downes (1969). In addition, they resembeled the marker swarms of *Aedes taeniorhynchus* (Wied.) described by Nielsen and Nielsen (1962) and the swarms of unknown insects reported by Wiersma (1966).

We also observed that *Ps. columbiae* males form at least 2 types of marker swarms. The most common one is the funnel-shaped marker swarm that is formed over markers which are not very elongate. The other type is a curtain-shaped swarm that forms over elongated markers such as shell roads and the light-colored gravel shoulders of blacktop roads. Provost (1956) reported *Ps. columbiae* males forming columnar marker swarms over

Table 1. Other insects captured over markers in swarms of male *Psorophora columbiae* occurring in east Texas ricelands, 1981–82.

Species*	Sex	Species*	Sex
Ae. sollicitans (Walker)	F	*Cx. salinarius* Coquillett	F,M
Ae. vexans (Meigen)	F	*Ps. ciliata* (Fabricius)	F,M
An. crucians Wiedemann	F	*Ps. ferox* (Humboldt)	M
An quadrimaculatus Say	F,M	*Ur. sapphirina* (Osten-Sacken)	F,M
An. walkeri Theobald	F,M	*Ataenius* sp.	Not Determined

* All Diptera: Culicidae save for *Ataenius* sp. which is Coleoptera: Scarabaeidae.

blacktop roads in Florida, but did not report any curtain-shaped swarms.

Although not observed in this study, *Ps. columbiae* may also exhibit ground swarming behavior. Ground swarming behavior was described by Neilsen and Greve (1950) as a common behavior for males of *Aedes cantans* (Meigen) in Denmark. Noises from mosquitoes flying in a concealed ground swarm might account for the sounds heard before marker swarming by *Ps. columbiae* became evident at the riceland sites used in our study.

The figure-8 pattern of flight followed by *Ps. columbiae* males while they are in marker swarms may be a modification of the circular path described by Neilsen and Greve (1950) for swarming *Ae. cantans* males observed in still air and low wind speeds. Also, observation of male *Ps. columbiae* reaction to wind while they were in the marker-swarming phase of their behavior support the observations of Neilsen and Haeger (1960) and Downes (1958) who reported that male mosquitoes face into the wind while swarming.

The downwind drift and lowering of male *Ps. columbiae* swarms seen during this study on windy evenings might be at least partially explained by changes in the distance of the swarming males from markers caused by increased wind speeds. For example, if the wind velocity exceeded the flight speed of the male mosquitoes causing the males to be carried downwind by the breeze and if, under these conditions, the males were able to maintain the same altitude, their distance from the marker would increase. With the increase in distance, it is inevitable that the apparent size of the marker would decrease in the eyes of the mosquitoes. If instead the swarming mosquitoes went to a lower altitude, their distance from the marker would not increase as much while being pushed downwind. Correspondingly, the apparent size of the marker would not seem to decrease as much to the mosquitoes as would be the case if they maintained the same altitude when displaced downwind from the marker. Another partial explanation might be as the height of the swarm decreases, the wind speed experienced by the mosquitoes would be reduced, thus the insects would be able to avoid further displacement by their downwind movement.

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References Cited

Charlwood, J. D. and M. D. R. Jones. 1979. Mating behavior in the mosquito, *Anopheles gambiae* s.l. I. Close range and contact behavior. Physiol. Entomol. 4:111–120.

Clements, A. N. 1963. The physiology of mosquitoes. Pergamon Press: Macmillan Co., New York, N.Y. 393 pp.

Downes, J. A. 1958. Assembly and mating in the biting Nematocera. Proc. 10th Int. Congr. Entomol. 425–434.

Downes, J. A. 1969. The swarming and mating flight of Diptera. Annu. Rev. Entomol. 14:271–298.

Edman, J. D., J. S. Haeger, W. L. Bidlingmayer, R. P. Dow, J. K. Nayar and M. W. Provost. 1972. Sexual behavior of mosquitoes. 4. Field observations on mating and insemination of marked broods of *Aedes taeniorhynchus*. Ann. Entomol. Soc. Am. 65:848–852.

Frohne, W. C. and R. G. Frohne. 1952. Mating swarms of males of the mosquito, *Aedes punctor* (Kirby), in Alaska. Mosq. News 12:248–251.

Horsfall, W. R. 1942. Biology and control of mosquitoes in the rice area. Univ. Arkansas Agric. Exp. Stn. Bull. 427. 46 pp.

Knab, F. 1906. The swarming of *Culex pipiens*. Psyche 13:123–133.

Meek, C. L. and J. K. Olson. 1976. Oviposition sites used by *Psorophora columbiae* (Diptera: Culicidae) in East Texas ricelands. Mosq. News 36:311–315.

Nielsen, E. T. and H. Greve. 1950. Studies on the swarming habits of mosquitoes and other Nematocera. Bull. Entomol. Res. 41:227–258.

Nielsen, E. T. and J. S. Haeger. 1960. Swarming and mating in mosquitoes. Misc. Publ. Entomol. Soc. Am. 1:72–95.

Nielsen E. T. and A. T. Nielsen. 1953. Field observations on the habits of *Aedes taeniorhynchus*. Ecology 34:141–156.

Nielsen, E. T. and J. T. Nielsen. 1958. Observations on mosquitoes in Iraq. Entomol. Medd. 28:282–321.

Nielsen, E. T. and J. T. Nielsen. 1963. The swarming habits of some Danish mosquitoes. Entomol. Medd. 32:99–170.

Nielsen, H. T. and E. T. Nielsen. 1962. Swarming of mosquitoes. Laboratory experiments under controlled conditions. Entomol. Exp. Appl. 5:14–32.

Olson, J. K. and C. L. Meek. 1980. Variations in the egg horizons of *Psorophora columbiae* on levees in Texas ricelands. Mosq. News 40:55–56.

Olson, J. K. and W. H. Newton. 1973. Mosquito activity in Texas during the 1971 outbreak of Venezuelan equine encephalitis (VEE). I. Vector potential for VEE in the Texas rice belt region. Mosq. News 33:553–559.

Pausch, R. D. and M. W. Provost. 1965. The dispersal of *Aedes taeniorhynchus*. IV. Controlled field production. Mosq. News 25:1–8.

Provost, M. W. 1953. Motives behind mosquito flights. Mosq. News 13:106–109.

Provost, M. W. 1958. Mating and swarming in *Psorophora* mosquitoes. Proc. 10th Int. Congr. Entomol., Montreal (1956), 2:563–565.

Provost, M. W. 1960. The dispersal of *Aedes taeniorhynchus*. III. Study methods for migratory exodus. Mosq. News 20:148–161.

Schwardt, H. H. 1939. Biologies of Arkansas rice field mosquitoes. Univ. Arkansas Agric. Exp. Stn. Bull. 377. 22 pp.

Sullivan, R. T. 1981. Insect swarming and mating. Fla. Entomol. 64:44–73.

Wiersma, J. H. 1966. Convection plumes and insects. Science 152:387.