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PRELIMINARY OBSERVATIONS OF FALL SWARMS OF CULEX PIPIENS L.1

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Introduction. This paper is a discussion of the natural history of male swarming of Culex pipiens L. in autumn in northern Ohio during and after the fall of the leaves of deciduous trees. This is a season of transition: temperatures are dropping, windiness increasing, mosquito breeding waning; the females are retiring into hibernation and the males inevitably aging as winter sets in. What happens from day to day at male swarming sites? Indeed, is the swarming phenomenon a purely summer exuberance to which full stop is put by autumn's frost, fall of the leaves, and windy threats of winter? For a period of 64 days, September 25-November 27, 1963, the swarming behavior of this species was kept under surveillance in an area of its abundance. More than a thousand swarms were looked at superficially and certain representative swarming sites were observed intensively, usually for 15 or 30 minutes of swarming. To answer, if only sketchily, what may be seen taking place at the swarming sites, I checked the size of swarms and the shifting locations of big aggregations relative to wind and sun and especially to loss of leaves of trees. I determined that mating goes on about as late in the season as swarming itself and noted such male habits at swarms as interference with mating pairs by supernumerary males, and grappling between males.

Swarming of C. pipiens, one of the best known mosquitoes, is a phenomenon reported of old from Europe and in the classical American mosquito literature, e.g., Howard, Dyar & Knab (1912-1917). Still, even in our day, as the recent invaluable review of mosquito swarming literature for which we are indebted to Nielsen & Haeger (1960) demonstrates, there has been no great leap forward to understanding the significance of the swarming habit. Chiang (1963), hinting we need more facts and less speculation, complains justifiably that public health students of crepuscular Diptera ignore the diurnal swarming of other than blood-sucking Nematocera. Drs.

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Nielsen & Haeger (l.c.), whose unwavering conviction it is that swarming and mating are unrelated habits, have attempted to reconcile their conviction with the reported data of others who oftentimes came to the contrary conclusion. If it can be shown, for I don't believe it ever has been, that mating takes place at a higher rate away from swarm sites during swarming than it does in the swarms, or what seems rather less likely, that there is a consequential amount of mating of swarming mosquito species at another time of the day, then the independence of mating from swarming will be practically established.

Males of C. pipiens, like some other mosquitoes, may visit flowers for nectar immediately after swarming (cf. Sandholm & Price, 1962). An intensive search for nectar feeding is desirable and this search should give attention to possible mating at or near flowers. At present, it seems to me, the "classical" assumption that swarming somehow subserves mating is the predominant view. However, I must confess to error myself in using such presumptive terms which beg the question, as "mating swarms" and "nonfunctional swarms," although these terms may become fully warranted in the future. For some mosquito species, mating is known only from observations made at swarms. Furthermore, every malariologist "knows" in his bones and marrow that if he has succeeded in establishing a self-perpetuating colony of Anopheles it was only because he could coax the males to swarm, whereupon they could plainly be seen mating at the swarms. Certainly, though, more data from Nature, "that dear riot of facts," are needed, and we may just as well accept Dr. Chiang into the swarming fold and learn all we can what the phenomenon is about, from diurnal swarms. Only more facts can bring the discordant interpretations into agreement to be "engraved on enduring bronze," a law of Nature. Then the Don Quixotes of both persuasions can bray together, "no rebuznaron en balde . . .

Observations: Area. All observations

were made on about an acre in Strongsville, Ohio, a rapidly developing town unit of the Cleveland conurbation. On the old Whitney homestead (where I live), onequarter mile east of Pearl Road intersection there flows a sluggish, weedy, little creek which bred the heavy mosquito population studied. Under the impact of domestic sewage pollution the erstwhile intermittent creek became permanent, fed by cesspool effluents, malfunctioning septic tanks and sanitary fields. Swarming sites, evidently excellently suited to \tilde{C} . pipiens, exist along the wooded creek, where still survive elements of the original beech-maple forest diversified by willow, ash, elm, honey locust, apple and wild cherry. The abundant aquatic insects are those two dipterous indicators of pollution, the rat-tailed maggot and the mosquito of this study.

Swarms. It is worth while for the sake of brevity to glance at the swarms as a whole before breasting discussion of individual observations, special topics and exceptions. When I began these observations September 25, it is reasonable to suppose swarming was already in decline, having been occurring at the same sites all summer. I watched whenever I was free at swarming times (chiefly sunset) during a period of 64 days. On 40 of these days swarms were actually found. For dawn swarms my record was not nearly so good as for evening swarms. Very likely a smaller swarming normally occurs at dawn on each day when there will be evening swarming until, as a result of frosty nights, it becomes too cold for flight at daybreak. However, it should be noted that I did encounter dawn swarms on November 22, a day without evening swarms.

I forfeited 5 days' observations to make a trip October 1-5. During this week the trees, which had been gradually acquiring fall tints, turned markedly red, yellow or brown and there occurred the second killing frost. The first had been the night of September 29-30. Besides the 10 possible swarmings of the days of my trip I also missed 10 evenings and

DECEMBER, 1964

24 morning possibilities. Some of these days were much too windy for swarming but on others swarming probably took place. Low temperatures at swarming times, while probably not a limiting factor here in summer, certainly prevent swarming many fall mornings and some fall evenings. In this study swarming was seen over the range 44-78 degrees F. Components of this range include: (1) September evening swarms . . . 53-71 degrees; (2) October evening swarms . . . 53-78 degrees; (3) morning swarms (none in September) . . . 45-61 degrees; (4) first magnitude swarms (magnitudes are explained below) . . . 49-71 degrees; fourth magnitude swarms . . . 44-57 degrees. In the final analysis, for the 128 potential dawn and sunset swarming occasions I actually observed swarms on 51 occasions, and saw that there were none on 33 occasions; for the remaining 44 occasions, I do not know.

Swarming periods differ in many respects, including: (1) size of swarms; (2) duration of period, which is discussed after a size classification of swarms has been explained; (3) locations favored; (4) activity level, i.e., flight state of languidness or frenzy; (5) mating; (6) grappling and other details of behavior.

Of primary importance is (1) size, a perplexing problem I dealt with semiobjectively by devising a "classification of magnitudes" (see below) which can be used to compare either swarms or swarming periods. Under (3) locations favored, is considered the shift to different sites at different points of the compass in keeping with changes in physical conditions, especially light and wind directions. (4) "Activity level," a conjectural variation of average speed of flight, troubles me, for I believe real differences exist both within a swarming period and between different periods, but I have made no effort to quantify them. (5) Matings for a swarming period were at best simply counted at one swarm for 15 or 30 minutes. (6) Grappling, which was not interpreted to include the interference of supernumerary males with mating pairs, was

only occasionally seen. Mating and grappling will be discussed presently. The solution finally adopted for expressing size of swarms is given in the next paragraph.

Classification of Magnitudes. During the field work, while counting and estimating swarms, I pondered over some way to be objective about size of swarms too large to count. The result was classification into four magnitudes: first magnitude swarms exceed 1,000 males; second magnitude swarms have several hundred but much less than a thousand; third magnitude swarms have over 10 but less than 100; and fourth magnitude swarms are little swarms of 1-10 males. The classification is practical and about as accurate as such observations support. It will satisfy advocates of Aristotle's dictum not to seek greater precision than the nature of the subject matter warrants. But a better means of measuring swarms must The estimates should be be devised. made during the 10-15 minutes about the middle of the period, but fortunately, any time during the second or third quartiles gives useful figures. Two or three of the largest low swarms should be chosen for counting. It is desirable to avoid any consistency in selection of sites counted on different nights or mornings if swarmings as well as swarms are being compared.

Such an index as the magnitudes classification of swarms might also be used to measure populations of C. pipiens. It would be practically worthless unless done repeatedly over a period of several weeks, however. This problem is perfectly familiar to mosquito workers who have used counts of Anopheles females in natural resting places, or biting rates of culicine pests or even light-trap collections to calculate populations. Used to support or check another density index, the swarm-magnitudes classification would be valuable. For example, during this study the biting rate was invariably virtually zero and had it been depended upon alone for a reconnaissance of C. pipiens density the species could have been considered rare.

Application of the classification to compare the size of swarms and the different swarming evenings gave a series of magnitudes declining gradually, presumably pari passu with decrease of the male population of the area. Rises interrupting the decline occur where conditions favor high-level activity of mosquitoes. There were thus 14 swarmings of first magnitude with peak estimates much larger than 1,000 males for the earliest 4. These heavy swarming dates were September 25, 26, 27, 28, October 6, 8, 9, 10, 11, 12, 13, 14, 21 and November 9. All of these were evening swarming periods. Swarms of less than first magnitude are comparatively much smaller aggregations. apt term of the classical literature, "smokelike," applies only to first magnitude swarms. The October and November first magnitude swarms were only fractions of the size of the 4 September ones.

Second magnitude evening swarms occurred on 13 occasions: October 15, 16, 17, 18, 19, 20, 22, 23, 25, 26, 27, November 6 and 10. Thus they were the next stage in the chronological decline of swarm size which was chiefly first magnitude in late September and the first half of October. However, there were the two noteworthy exceptions, first magnitude swarms of October 21 and November

Third magnitude swarms are a mixed lot resulting from diverse causes. Three main types may be recognized: (a) September and October windy evenings . . . swarmings of September 29, 30, October 7, 24; (b) October and November morning swarms . . . swarmings of October 8, 17, 24, 27 and November 10; (c) Swarms of the latter half of November when lower densities evidently permitted no larger aggregations than third magnitude . . . November 17, 26, 27.

Fourth magnitude swarms are divisible into: (a) Morning swarms . . . October 22, 23, 25, 26, November 22; and (b) Evening swarms damped by strong wind or low temperature . . . October 28,

November 4, 16, 19. However, the fourth magnitude swarming of November 21 must have been impeded by some unrecognized adverse factor, for the temperature was 50 degrees and the air quite calm.

Duration and genesis of swarming can most conveniently be considered together. On different occasions swarming was observed to last from 10-65 minutes. The figure calculated for most swarms is too short. Dawn swarms seen for the entire period never exceeded 25 minutes. The evening swarming periods observed from beginning to end were most commonly about 40 minutes' duration. Greater precision with longer periods would have been possible to achieve with several helpers to detect earliest and latest swarming.

It is most reasonable to estimate 30 minutes maximum for dawn and 65 for evening swarming occasions. Plotting number of swarmers against time at an individual swarm gives an irregular normal population curve. During the first quartile males are almost constantly arriving at and leaving a common resting place at the core, but the active swarmers are increasing and actual resting at this spot is usually limited to the first ten minutes of swarming. During the third quartile, the curve plainly shows, some swarmers quit swarming. A peak is passed close to, often slightly beyond, midpoint of the swarming period.

It is clear the time spent swarming is different for different swarmers. It is also not necessarily the same for different swarms. The exodus of swarmers, which is not to be confused with merely changing from one to another swarm, was actually carefully observed in the fourth quartile. The males which depart then are usually quitting swarming for the period, and they depart in a beeline directly away from the swarm. Perhaps they are going straight away to flowers for nectar. No male ever remains resting on the tree after the breakup of swarming.

Swarming and Foliage Changes, Al-

most every deciduous tree in the study area manifested some color change, usually to yellow, red or brown, before dropping its leaves. Fall colors were brightest in a week or ten days following the overnight frost of September 29-30. There were swarms every evening October 6-28; the first eight evenings were first magnitude swarming. Thus conditions favored discovery of any marked effect of change of leaf color. No effect whatsoever was noticed. For example, a red maple tree with 16 good swarming sites had the same usually large and similarly distributed swarms during and after the spectacular turn of its foliage to crimson. Nor did yellow or brown leaf color appear to impair suitability of a site. Wild cherry leaves turned sere and brown soon after the second frost, but as would be expected from experience with the bulldozed dead wild cherry there was no obvious reduction in swarming while the brown leaves hung on. This finding was confirmed and extended with reference to other kinds of trees and even to other colors, e.g., the luxuriant foliage of the ashes which persisted relatively long developed a strikingly beautiful purple, yellow and green color scheme, but swarming there proceeded very much as before the complementary purple and yellow pigments appeared.

Loss of leaves, on the contrary, quite unlike change of foliage color, did produce noteworthy effects on swarming. Decreases in size of swarms immediately followed loss of some leaves at or near the tips of branches serving as markers. And as soon as the branch tips became quite bare swarming at that site ceased altogether. However, this diminution of sites increased swarm size at trees, e.g., willows, an apple, whose leaves persisted longer, and at buildings and permanent natural sites of swarming which now obviously "captured" swarmers as the tree sites were annihilated. Some of these which had been relatively poor markers, such as locust pods, the "tent" of Malacosoma americana and the sites of the bulldozed wild cherry tree now carried larger swarms than in the September heyday of first magnitude swarms.

As with leaf color changes I chronicled much detail on the effects of the fall of leaves. The conclusion is so straightforward and clearcut, however, viz. that loss of leaves gradually and finally utterly destroys a swarming site, that the readers will be spared these data. The rate at which leaves fell and/or turned color was probably speeded by dry weather. The U. S. Weather Bureau reported September and October 1963 the driest autumn for a decade in the region. The total lack of rains which could have flushed the breeding areas in early October allowed an ultimate small brood to emerge which also favored these observations of fall effects on swarming. As a matter of fact, scarcely any rain fell from September 25 to October 27. Thus, as trees lost their leaves, swarming ceased there, though it continued at other undisturbed sites until the day before Thanksgiving (November 27) when the latest swarms were seen. On this last day the only swarming sites in use at trees were the willow trunk and the persistently leafed dead wild cherry. Buildings and the concrete slab of the bridge had their usual swarms.

Mating at Swarms. I think mating has been a rather neglected subject in mosquito swarming studies. The causes may lie not so much in its demands on time or effort as the embarrassing solicitations of the curious, e.g., old lady: "Are you all right?" This can't be answered: "I'm O.K., Jack." Or of the omnipresent small boy: "What ya doing down there under a flock of old bugs?" This could be answered: "Beat it!" Watching for mating at a swarm ties the observer down and interferes with daily reconnaissance of the study area. Mating was neglected in this study too.

For three weeks I hopped about excitedly making little discoveries of idiosyncrasies of *C. pipiens* swarms. I needed all this time to keep *au courant* of their

reorientations to various changes of markers, varying wind and light. Finally on October 12, having peered at the swarms of 12 evenings and one morning very much on the move, I accidentally saw a mating pair leave a swarm. Next evening I saw another pair.

Impressed at last that something essential was being overlooked, I began allotting 15 or, if possible, 30 minutes to give undivided attention to a single swarm, not consistently the same swarm, but the largest one at the same tree. This was the dead wild cherry which had been torn up by the roots, bulldozed to a secluded place and toppled over where I could conveniently and privately lie prone on my back under swarms only 2 to 8 feet overhead. They were usually small swarms of second or third magnitude. The leaves had dried on the branches without detaching, so that this group of about ten swarming sites persisted while at other trees they were annihilated by leaf-fall. The actual counts of mating pairs seen during the first 15 days when there were swarms every night (October 14-28) were chronologically: 6, 6, 4, 4, 2, 3, 8, 12, 5, 6, 0, 1, 3, 13, and o. These data manifestly show mating consistently taking place. And the pitfalls of counting pairs are mostly errors of omission.

Mating can be regarded as characteristic of fall swarms of C. pipiens. The two evenings with no observed pairings were to be expected, for the order of magnitude of those two swarms was fourth, i.e. there were only 1-10 males present at peak. The two evenings with the maximum counts of matings were just as unsurprising in that they were quite large. One was barely but surely first magnitude, the other second magnitude. I have previously made use of socalled mating rates, the number of matings observed per unit of time. In the present preliminary study the data are too few, the figures too small, the samples inadequate for calculation of rates, but there is nothing hypothetical about their reality. Moreover, pairing occurs over the whole period of swarming. Mating is therefore

a perfectly natural occurrence in fall swarms. It was seen sometimes in "spurts." One had the impression one pairing "sparked" further pairings. Over half the pairs counted were being annoyed by supernumerary males.

While watchfully waiting for mating pairs I noticed and followed the development of swarms, the exodus from them and grappling between males. But all these observations were made at evening swarms, under the growing impression that dawn swarms were small and of short duration so that little or no mating there was likely. This was rank rationalizing; I scarcely ever could find time observe dawn swarms intensively. However, on Sunday morning, October 20, spying a pair near the close of the swarming period, I lay down there and watched for only an additional 7 minutes of rapidly waning swarming and saw 3 more pairings. Thus it appears not unlikely that mating takes place at dawn swarms just as in evening ones.

Swarm Types. The typical swarm of C. pipiens of this study has a rather diffuse core of swarmers a few inches to a foot below the marker, which is usually a tuft of leaves at the very tip of a tree branch. Additional males fly up in disarray to a distance of two or three feet from the core. The males face as much as they can toward branch-tip marker and tree trunk except when leaving the They fly upwards, then fall irregularly, then repeat the process. They are blown out of position by gusts of wind, can be induced to leave also by a shout or passage of the insect net through the swarm, but will regroup as soon as the disturbance ceases.

Swarms form at markers at north, south, east and west aspects and intermediate points all about a small tree standing apart from others, but the largest swarms will be away from the sun and wind of the particular occasion. An odd fact is that even though there is no wind during swarming the swarmers orient themselves at that side of the tree so as to form the largest swarms just as though the

wind which blew earlier in the day or during the night were still blowing. Occasionally a male switches to another swarm on the same tree or another tree. He then orients his body axis appropriately for the new swarming site which may be quite different from his previous axis of orientation.

Though the several swarms at a small tree are almost bound to be oriented differently since all point inwards toward the trunk, that swarm which is away from sunset or sunrise, especially if it chances to be away (sheltered) from whatever breeze may be upsetting the calm air, will be the largest. Trees growing in juxtaposition have no swarms where they adjoin one another. Except in windy weather swarms are discovered most easily on the edges of clearings facing away from the sun and shielded from the prevailing wind. Calm air is a most important prerequisite and wind in excess of about five miles per hour, unless intermittent, eliminates swarms on exposed sites.

Some markers will generate swarms up to first magnitude, but others seem able to induce at best only little ones of third or fourth magnitude. When mosquito activity is at low intensity or density low, the poorer markers can often still be spotted because minuscule swarms occur or individual swarmers tarry there between switches. With mosquito activity very high and the air quite calm, all sites will have swarms and some branch tips not known to be markers will at times attract a few swarmers. Then too, induced swarms may swarm even at the observer, particularly behind or before his head. The largest swarms tend to form nearest the breeding areas, if not immediately over them, probably because C. pipiens does not migrate.

A generalization that species of trees become increasingly suitable for swarming the larger their leaves, the more luxuriant the foliage, grew out of a search for favored *species* of trees. Evidently, however, any species will serve, but the small-leafed open kinds are least suitable. Even

red cedar (Juniperus virginianus), the species at the foot of the suitability order list, had two small swarms on one evening of first magnitude swarming. There are five old red cedars in our front yard and no other trees so that there was no alternative choice except the house itself for swarmers.

Trees provide most of the natural swarming sites, but the house mosquito also swarms about buildings close to its larval habitats. Each of the corners of such a house, provided none is shaded by a tree, will apparently invariably harbor swarms when the trees thereabouts do. That corner away from sun and wind will have the largest swarms. may also be swarms almost as large at the ends of the peak of the roof and on good swarming nights swarms of corners and peak ends will be connected by a continuous "fringe" of swarmers. Windows, too, though they entirely lack projections to serve as markers (comparable to branch tips), have swarms on favorable evenings, especially on the side of the building away from the sun. Obviously, the concept of a marker including a projecting point breaks down in many of these artificial sites.

Later on, after the trees had dropped their leaves, swarms were seen on several occasions along the trunk of a willow and along two telephone poles. Again no marker points were evident. Swarms also regularly occurred in front of the flat slab of concrete topping the road bridge. This last swarming site has an additional distinction. It is at ground level.

Elevation of sites was highly variable. Apparently any height above the ground from a couple of feet to at least 40 feet might be suitable. Swarms at various elevations formed at much the same times, i.e., nothing similar to the "ascensions" described by Nielsen & Greve (1950) was seen. At breakup of swarming, the beeline departure path of males was virtually horizontal. Markers odd from a human point of view were: clusters of big pods of honey locust; a "tent" of Malacosoma americana; the upturned roots of the

dead wild cherry; the carburetor of a vellow tractor; the tailgate of a red pickup truck. All of these peculiar sites were used over and over.

SUMMARY. Fall swarming of Culex pipiens L. males on 40 days of the period September 25-November 27, 1963 is described from Cleveland, Ohio.

1. More than a thousand swarms were estimated seen during the 64-day

2. Swarming occurred over a temperature range of 44-78 F. on calm mornings and evenings in twilight.

3. Trees provided the natural swarming sites, but swarming also took place about buildings and certain large objects.

4. A practical size classification of the swarms and swarming periods into four magnitudes was devised by application of which a decrease in swarming was manifested as the season advanced.

5. Maximum duration of evening swarming was estimated at about 65 minutes, of morning swarming to be about 30 minutes.

6. The autumn change of leaf colors had no obvious effect on swarms

and swarming.

7. Fall of the leaves reduced and then annihilated typical swarms at branch tips, chiefly in October. Swarming continued at other sites until November 27.

8. Mating was seen at beginning, middle and end of swarming of evening and morning. It is viewed as a normal activity at swarms.

9. About half the mating pairs were annoyed by supernumerary males.

10. Grappling of two or rarely three swarming males was occasionally seen.

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See Page 461 for outline of program of Annual Meeting in Tampa, Florida, March 14-17, 1965