

THE UNIVERSITY OF MANITOBA

STUDIES ON THE DISPERSAL AND SWARMING BEHAVIOUR OF
AEDES MOSQUITOES IN SOUTHERN MANITOBA

BY

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ABSTRACT

The dispersal of Aedes mosquitoes was studied in southern Manitoba using both a dye and a radioactive ^{32}P marking method. The results suggest that part of the Aedes vexans populations studied remained within 4 km of the emergence site. Part of the emerging population is migratory, as was shown by a number of marked recoveries near the edge of the trapping grid shortly after emergence. Aedes communis appears to be a sedentary species, although there is less evidence for this in the present study.

The refractory period of marked Ae. vexans and Ae. communis females was studied. Both species were found to have a refractory period of 5-8 days and this appeared to affect the movement of both species by inhibiting dispersal until mating had occurred.

An evaluation was made of marking and recovery methods. Dye marking was found to be superior to ^{32}P marking because dye marking permitted one to gather information on insemination and had the potential for other studies. The New Jersey Light traps and the Chant-Baldwin 7 watt traps were found to be equally effective in collecting adult mosquitoes and varied only in the labour and time requirements in the laboratory and the field.

Swarming behaviour of Ae. vexans was studied during 1975. Male Ae. vexans were found to swarm in the evenings in marker swarms which were generally all Ae. vexans. Ae. vexans was found to swarm with other species in top swarms but was usually a small component of these swarms.

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Chapter I

INTRODUCTION

A) Dispersal

The term disperse is defined by the Oxford dictionary as "scatter, go, send in different directions". When referring to mosquitoes, this definition fits one of the two major means of movement viz migration and dispersal. Provost (1953) discussed mosquito flight and determined two separate "motives" for flight and movement away from a breeding site. The first, dispersal, occurs when a mosquito begins to fly about in search of a means of satisfying a physiological need. These ~~means~~ include satisfactory resting sites where light and hygrothermal environment are ideal, a nectar source for sugar feeding, blood meals, suitable oviposition sites for females, and the search for suitable swarming sites for males. This movement has been defined as appetential flight by Provost, a flight in search of some means of satisfying an appetite brought about by some neurological imbalance which produces searching (flight) behavior. Appetential flight results in the random movement of adults from the pools in which they developed.

The second type of movement away from a source is described by Provost as migration, a term that has often been used interchangeably with dispersal by research workers. To migrate is defined by the Oxford dictionary

as "to move from one place to another" or in reference to birds and fish as "to come and go with the seasons".

Provost defines migration as non-appetential flight, or flight undertaken not in search of a means to satisfy some physiological need, such as food or shelter but flight which is undertaken to satisfy the need to be in flight. Non-appetential flight will continue until some intrinsic mechanism stops it, often after carrying a large number of adult mosquitoes long distances. After the end of migration, an individual mosquito will then begin appetential dispersal in search of nectar, blood meals or some other physiological requirement.

The basic purpose of the present work was to investigate dispersal from a breeding site. Therefore, migration, its causes and its results, will not be discussed in any detail, except where it has some bearing on the study of appetential flight.

Schneider (1962) discussed the effects of dispersal on a population of insects emerging at the same time from a single source. First, the length of the mean distance between individuals in a population is increased as the distance from the breeding site is increased. This is in response to the search for food. After this, the mean distance between members of a population decreases again as they begin to concentrate about the best feeding, resting and oviposition sites. Conditions in the area will affect the direction and distance moved by a dispersing

population. Gillies (1961) found that the dispersal of a marked population of Anopheles gambiae Giles in East Africa, was related to the density of human settlement in the region. In areas where the human population was high, less dispersal took place than in areas where the human population was low. Individual An. gambiae entering an area of high human populations did not continue to move after they had come into contact with man. This picture of dispersal in An. gambiae remains similar to that proposed by Schneider. Adults emerging near human settlements undergo only a fraction of the initial dispersal phase before they begin to concentrate about human settlements.

Dispersal, by spreading a population over its habitat, is a function vital to the survival of a species (Klassen, 1968). Some individuals may move into areas where they will undoubtedly perish, as described by Wright (1918) when a ship, 25 km off the Arabian coast was invaded by Anopheles pulcherrimus Theo. Also Kirkpatrick (1925) reported that Anopheles pharoensis Theo. flew 72 km into the Egyptian desert to invade an army camp. Although these individuals would perish under normal conditions, one must assume that part of the population flew in a favorable direction and survived. Klassen (1968) concluded that dispersal helps to prevent the extermination of a species due to local changes in weather and climate. By dispersing widely, some members of a population will

increase their chances of finding a suitable environment and consequently produce another generation. Southwood (1962) described dispersal and migration in terrestrial arthropods as being a behavioral response to an unstable environment. Brown (1951) found much the same behavioral response in aquatic insects. Animals living in an unstable environment, one which may or may not be present for the next generation to occupy, tend more toward dispersal, thus increasing the chances of some members of the population finding suitable habitation. Klassen (1968) discussed the benefits of dispersal to a population of mosquitoes in an unstable environment and concluded that the rapid gene flow that would result from such dispersal would result in a larger gene pool, allowing the mosquito population to survive under new conditions of climate, vegetation and changing patterns of human settlement.

B) Swarming

Swarming is a process in which adult insects, usually male, aggregate in flight around a defined area. Swarming is found in many dipteran families, including the Culicidae, as well as other insect orders. The ecological function of swarming has been determined to be epigamic behaviour, by which males make themselves available for copulation with virgin females. However, the function of swarming in mosquitoes has not been definitely determined and is subject to considerable debate. Only the swarming of the Culicidae will be considered here.

Chapter II

LITERATURE REVIEW

A) Dispersal

1) Culex species

Several studies have been conducted on the dispersal behavior of Culex species. Bailey et al. (1965) studied the dispersal of Culex tarsalis Coquillett in the Sacramento Valley of California. Over a period of three years, 18 releases were made in and about the rice fields that act as breeding sites for this species. Bailey et al. found that C. tarsalis dispersed in all directions at low wind speeds (less than 3.2 km/h). From 3.2 - 6.4 km/h dispersal was upwind and above 6.4 km/h dispersal was downwind. They also found that about 10% of a marked population of C. tarsalis dispersed in a direction different from that of the main body of flies. Marked adults were captured up to 25.7 km from the release site (R.S.). Bailey noted that when this species emerged from rice fields or were marked and released from cages early in the evening, the adults would rise in a spiral to 3.6 or 4.6 m and if the wind was over 8 km/h be carried off downwind, over hedges, trees and other obstacles. Only a few remained near the ground level and attempted to fly upwind. The majority of adults captured were in a downwind direction and Bailey concluded that effective dispersal was almost always in this direction.

Reeves et al. (1948) found similar results with C. tarsalis, also in southern California. They recovered this species downwind at distances greater than 3.2 km.

Other studies have shown that Culex nigripalpus Theo. will disperse up to 5 km (Dow 1971). Clarke (1943) studied the dispersal of adult Culex pipiens L. emerging from a New Jersey marsh and found they dispersed up to 22.5 km from the R.S. and as much as 15.3 km in a 24-48 hour period. Clarke did not discuss the effect of the environment on dispersal but felt that C. pipiens dispersed as far and as fast as other species present (Aedes vexans Meigen, Culiseta inornata Williston and others).

2) Aedes species

A number of studies on the dispersal of Aedes mosquitoes have been conducted. These include anecdotal comments on long range dispersals into areas not normally occupied by adult mosquitoes, and detailed studies using mark and recapture techniques. Among the earliest reports was one by Curry (1938) who reported capturing wind blown Aedes sollicitans (Wlk.) aboard a ship 177 km off Cape Hatteras. Curry traced, by using weather charts, their probable origin to a location on the coast of North Carolina.

The dispersal and migration of Aedes taeniorhynchus (Weid.) has been studied more extensively than that of any other species. Provost (1952, 1957) was the first to in-

investigate the dispersal of this species in southwest Florida. Conducting his experiments on a series of low islands adjacent to Sanabella Island, Provost found that females move up to 32.2 km from their release site. Provost showed that Ae. taeniorhynchus is a migratory species, often exhibiting strong "non-appetential" flight away from its breeding sites, always on the first night after emergence. Provost concluded that dispersal of Ae. taeniorhynchus proceeded with or without migration, and occurred after migration started from the spot where migration ended; and that dispersal covered only relatively small areas and adults did not cross large expanses of water, and dispersal is limited to the island on which it starts.

Elmore and Schoof (1963) and Bidlingmayer and Schoof (1957) studied the dispersal of Ae. taeniorhynchus near Savannah, Georgia. They found that the adult females dispersed up to 32 km from the R.S., but that 61% of marked recoveries in 1957 and 50% in 1963 were recovered within 3.2 km of the R.S. and 77% in 1957 and 73% in 1963 were recovered within 6.4 km of the R.S., thus strongly indicating that the majority of individuals did not move beyond this point. Recovery beyond 6.4 km did not occur until the 4th night after release. Adult males were captured up to 3.2 km from the R.S.

The dispersal and longevity of Aedes melanimon Dyar was studied by Kliever and Muira (1969). No marked adults

were released in this study but by following the movement and occurrence of adults from their only known breeding sites, Kliwer and Miura were able to show that a significant number of adult Ae. melanimon was capable of moving up to 2 km downwind from their breeding area. The greatest number of adults was present at the source and within 4.8 km of the source. Individuals were captured up to 90 days after emergence at the breeding site. Kliwer and Muira also found that a few individuals moved in directions other than that of the prevailing wind.

Causey et al. (1950) and Causey and Kumm (1948) studied the dispersal of forest mosquitoes in Brazil. They found that marked Aedes serratus (Theo.) were capable of dispersing up to 11.5 km, Psorophora ferox (Humboldt) up to 10.8 km, Aedes terreus, (Walker) and a Wyeomyia sp up to 5.7 km. All recorded dispersal by marked adults was in the direction of the prevailing wind.

The dispersal habits of Aedes species in more temperate and boreal regions have also been studied. Hocking (1953) studied the flight habits, speed and range of several species of northern Diptera, including Aedes campestris Dyar and Knab, Aedes communis (Degeer), Aedes impiger (Walker) and Aedes punctor (Kirby). Hocking calculated the flight ranges of these species by the use of a flight mill. He found that Ae. campestris was capable of flying 53 km nonstop, Ae. impiger 48 km, Ae. punctor

46 km and Ae. communis 22 km.

Several studies have been conducted on the dispersal and longevity of Ae. vexans in various areas and under different ecological conditions. Stage et al. (1937) studied the dispersal of Ae. vexans and Aedes sticticus (Meigen) in the Columbia River Valley of Washington state. The area studied, (now largely flooded following the construction of dams on the river) was bounded by high mountains which reduced wind and produced numerous small waterfalls which kept the local humidity high. These conditions are ideal for the survival of adult mosquitoes. Stage found that most male and female Ae. vexans dispersed about 3.2 km with males dispersing more slowly than females. Maximum distance dispersed, based on the distance from the nearest breeding sites that unmarked adults were found, was 40 - 48 km. Ae. sticticus, on the other hand, had a usual dispersal distance of 8 km with a maximum dispersal similar to Ae. vexans. Adult females of both species were found up to 52 days after emergence and males up to 24 days. Gjullin et al. (1950), working in the same area, found the life span of the male and female Ae. vexans to be 90 and 100 days respectively; male and female Ae. sticticus lived 65 and 94 days. Stage et al. (1936) found that the 0.8 km across the Columbia River was easily bridged by the dispersing adults, with marked specimens being found on the other side within 24 hours after emergence. They considered that the dispersal of a population of Ae. vexans and Ae. sticticus,

emerging together from one site, was directly related to the size of the population: the greater the number present, the further the dispersal distance.

Clarke (1943) marked young adult Ae. vexans at their breeding site in a 16.2 hectare marsh. He captured males and females up to 22.5 km from the R.S. and recovered a total of 86 (35 males and 51 females) marked adult Ae. vexans. Clarke recovered 17% of the marked adults between 1.6-8 km from the marking site; 42% within 8-16 km and 41% between 16-24 km of the marking site. Recaptures were made up to 10 days after marking and up to 22.5 km from the site. On the first day after marking, Ae. vexans were captured out to 22 km from the release site.

Horsfall (1954) reported a migration of Ae. vexans into central Illinois. The invasion occurred in an area of Illinois with no known breeding sites of Ae. vexans. Horsfall proposed that the invading adults had entered the area on an advancing cold front from breeding sites between 145-370 km away. Subsequent information on this migration indicated that some of these adults may have migrated as far as 740 km in 24-48 hours.

Dispersal in Ae. communis has been studied by several authors. Jenkins and Hassett (1951) studied the dispersal habits of this species in the tundra and taiga biomes at Churchill. Jenkins and Hassett found Ae. communis to be a relatively sedentary species, rarely dispersing

beyond 1.6 km from its breeding site. The average distance dispersed by males was 149 m and females 175 m. The furthest distance from the R.S. that an adult was recovered was 1524 m. They also found that the direction of dispersal was not influenced by the wind. Nielsen (1957) claims similar dispersal habits for Ae. communis in the Rocky Mountains of Western U.S.A. Nielsen made "detailed studies on the flight range" and found the distance dispersed to be generally less than .40 km. These findings support those of Hocking (1953) who found that Ae. communis had a flight range of less than half that of other species he studied.

Other studies into the flight range of Ae. communis have shown somewhat different dispersal patterns. Vinogradskaya (1970) reported maximum dispersal of 29 km from a release site in Siberia. Vinogradskaya found that dispersal was directed by local wind conditions with maximum displacement occurring with the wind. Petruchuk (1972) found that Ae. communis adults dispersed 7-8 km over taiga landscape with the greatest dispersal occurring in high areas with numerous small river valleys. The adults dispersed along the river valleys, travelling more readily there than on flat terrain. Similar results were obtained by Klassen and Hocking (1964) with Aedes cataphylla Dyar and other species, near Edmonton, Alberta. Chant and Baldwin (1972) at Chalk River, Ontario, found evidence indicating that Ae. communis dispersed considerably more than

1.6 km. Their traps did not recover any marked adults until 18 days after release and then only at the most distant trap sites. They suggest that adult Ae. communis disperse quickly out of the release area and only later return to the area of the traps in response to CO₂ and light.

Shemanchuk (1955) studied the dispersal of Aedes flavescens (Muller) in Alberta. He recovered marked adults up to 10.6 km from the R.S. and for 33 days from the release date. Dispersal from the R.S. was largely downwind with males dispersing much shorter distances than females.

B) Factors affecting dispersal of a species

1) Behaviour

The potential for movement exhibited by a species of mosquito can be expected to affect the actual distance of dispersal experienced. Some species, such as Ae. taeniorhynchus, have been shown to be migratory under certain environmental conditions and therefore populations can be expected to move great distances when environmental conditions are suitable. Some tundra species, Ae. impiger, Aedes hexodontus Dyar, and Aedes pullatus (Coquillett), have strong flight habits which allow them to survive in an environment with sparse vegetation and strong winds (Nielsen, 1957). Other species, such as Aedes aegypti (L.) do not move very far from their source. Christophers (1960), citing literature sources, reported that Ae. aegypti

rarely moves far from the stable environment provided by human habitation where it mates, obtains blood meals and oviposits.

Hocking (1953), using a flight mill, found that Ae. communis flew less than one half the flight distance of other tundra species studied. His results confirm the field studies previously discussed which demonstrated that Ae. communis is a relatively sedentary species.

2) Local conditions

The ability of an area to provide all the needs of a non-migratory species would affect its rate and distance of dispersal. Migration, as described previously, is not affected by appetential flight. In an area with abundant nectar and blood sources, as well as mating, oviposition sites and shelter, one would expect a reduction in the number and length of appetential flights, and consequently a reduction in the dispersal of the population. Not only would the individuals in a population move about less, they would be less likely to have their flight affected by environmental conditions (Klassen, 1968).

3) Wind

Wind has been shown to be the most important environmental factor affecting the dispersal of mosquitoes. The effect of wind on specific species has been described earlier by Provost (1952, 1957), Bailey et al. (1965), Reeves et al. (1948), Currey (1938), Kliwer and Miura

(1969), Elmore and Schoof (1963), Causey et al. (1950), Causey and Kumm (1948) and Bidlingmayer and Schoof (1957). Wind affects the dispersal of mosquitoes and other insects when it inhibits or induces flight, and when it prolongs, curtails or channels a flight that is underway.

Kennedy (1939, 1961) described the effect of wind on the flight behavior of mosquitoes and other insects. Kennedy found that an insect in flight has a preferred rate of forward to backward movement of visual stimuli across the retinal field. Therefore, an insect taking off in a gentle wind will climb to a height which, combined with its preferred air speed, will produce the favored passage of ground images across the retinal field. An insect will make compensation in flight for transverse motion and changes in wind velocity which may interfere with the preferred rate. Kennedy found that an insect can adjust in one of several ways if the forward or backward movement of images is too great; by reducing air speed, flying higher which makes the ground images appear to move slower, turning into the wind or settling. When forward to backward movement is too slow, the insect can react by flying faster, flying lower, turning downwind or settling. In general, Kennedy found that as wind speed increased, the maximum height of upwind flight decreases as this allows for a smaller amount of forward movement to produce the proper amount of forward to backward stimulus on the retinal field.

For the same reasons, as wind speed decreases, maximum height of upwind flight increases.

Klassen and Hocking (1964) expanding on Kennedy's results and using data from Hocking (1953), attempted to describe the flight movement of Ae. punctator. In general their information is similar to that of Kennedy, for as wind speed increases maximum height of downwind flight increases and as wind speed decreases, height of downwind flight decreases so that the preferred retinal stimulation occurs. Klassen and Hocking found that above a certain height and wind speed, an insect is no longer able to control its movements and so turns and flies downwind, out of contact with the ground. For Ae. punctator, Klassen and Hocking found the visual stimuli produced by the interaction of flying at 76 cm above level ground and 150 cm per min. air speed to be the boundary at which controlled flight is lost. Taylor (1958, 1960, 1974) proposed the concept of a boundary layer, the height above ground above which wind speed equals the flight capacity of an individual insect. This boundary layer would vary from time to time with changes due to ground conditions and the species of insect involved. Above the boundary layer, an insect loses contact with the ground and control of its flight direction, so it flies downwind. After flying above the boundary layer, an insect can only leave it by actively attempting to fly lower or if some atmospheric condition brings about a disruption of the layer.

4) Temperature and humidity

Although temperature and humidity do not directly affect the distance of dispersal in a population of mosquitoes, hygrothermal conditions in an area do affect the activity of individuals and therefore their potential for dispersal.

Wright and Knight (1966) found that 93% of all Aedes trivittatus (Coq.) taken in traps were captured at relative humidities (R.H.) between 40-90%, indicating that this species was active at all R.H. within the normal daily range. Dow and Gerrick (1970) found that the activity of Cx. nigripalpus could be correlated to the R.H. at one hour after sunset, but no correlation could be found between the activity of Ae. taeniorhynchus and relative humidity. Platt et al. (1958) found the optimal humidity for Ae. vexans in Georgia to be 70%, while other species studied had an optimum ranging from 60-90%.

Rudolfs (1923) found that the effect of R.H. on flight activity of Ae. sollicitans and Aedes cantator (Coq.) was directly related to the speed of the wind. At wind velocities below 6.4 km, activity increased up to 75% R.H., but the activity curve flattened out at higher relative humidity. With wind speeds of 6.4-13 km/h the activity curve increased up to about 80% before flattening and above 12.8 km/h activity decreased with increases in R.H. until 85%, after which activity began to increase again. Rudolfs found that, in general, mosquito activity

increased up to 75% R.H., was constant between 75-85%, and decreased above 85%. Similar results were found for Cx. pipiens by Rudolfs.

Taylor (1963) investigated the effect of temperature on the flight activity of 15 species of insects, including 10 dipterans, and found that there was little difference in an insect's flight performance with increased temperature, once the lower threshold of temperature for flight had been reached. The lower threshold varies with species. Taylor concluded that, within the limits set by heat and cold tolerance, the flight activity of an insect is regulated by the length of time the temperature remains within those limits of the species each day. This activity is of course, limited by the favorability of other factors such as wind, light and humidity.

C) Swarming

Mosquito swarms tend to form in relation to some outstanding landmark, the swarm marker. The swarm marker may be any prominent feature of the landscape, including trees, branches, bushes, haystacks, farm animals, roadways or pond and lake edges (Downes, 1969). Nielsen and Nielsen (1963) describe two basic types of swarming behavior: the preliminary swarm and the definitive swarm. Preliminary swarms, first described by Nielsen and Greve (1950) in Aedes cantans (Meigen) occur earlier in the evening than definitive swarms, generally near the ground and not over

a marker. Preliminary swarms may result from some disturbance, often caused by an animal walking through grass or bushes where the males are resting (Nielsen & Nielsen, 1963). This disturbance stimulates a brief flight amongst the males. Definitive swarms, the typical marker-orientated swarms, are separated into four classes by Nielsen and Haeger (1960), based on the type of swarm marker utilized. Top swarms are formed above or to one side of some vertical object, the marker ranging in size from a tuft of grass to a church steeple, with many variations being described in the literature. Marker swarms form above some horizontal surface with a colour or brightness contrast serving as the marker. The swarm markers for marker swarms vary greatly in size. Downs (1955) produced Culicoides swarms of this type by placing dark coloured cloths on a roadway. Using white sheets Downs (1958) was able to produce swarms of Ae. hexodontus, Ae. flavescens and Aedes excrucians (Walker) over tundra at Churchill. Free swarms form above an area of level ground with no visible marker, at least to the observer (Nielsen and Haeger, 1960). All three types of swarms mentioned above have been reported to contain between one and many thousands of males all flying relative to the swarm marker (Nielsen and Haeger, 1960). A final type, the ceiling swarm, forms when large numbers of high flying males form a canopy with columns sometimes extending to ground level (Nielsen and Haeger, 1960). Nielsen and Nielsen (1963)

have observed other types of swarms, but these all appear to be modifications of the four types mentioned above.

The function of swarming has been the subject of some debate. Downes (1958, 1969) supports the idea that swarming is epigamic behaviour whose function is to bring together the sexes of a dispersed population. Males gather about some outstanding landmark, which is also attractive to females, and couple and mate with the females as they come near the marker. Recognition is by way of auditory response to the wind beat frequency of the females, as shown by Roth (1948) and possibly to some contact stimuli as shown in the subgenus Stegomyia by Nijhout and Craig (1971). Swarm mating has been observed in a number of species (Downes, 1969) including modified swarms where the swarm marker is also the host, as has been demonstrated in India with Aedes albopictus (Skuse) by Gublen and Bhattacharya (1972) and by Hartley (1971) in Ae. aegypti. In such cases, females coming to feed are mated by males that swarm about the host.

Nielsen and his co-workers do not consider swarming to be the major site of mating activity in mosquitoes. Their argument is based on a series of observations: swarms are often not species specific and males are not particularly good at discriminating between females of one species and another; because of this, a considerable amount of time and energy can be used by swarming males in attempts

to mate with females of other species (Nielsen and Haeger, 1960). In studies where the increase in mated females over time has been compared to the number of observed couplings occurring in swarms, the number is not large enough to account for the percent mated, as is shown by Kliever et al. (1967) in Aedes nigromaculis (Ludlow) and Ae. melaninon. Nielsen and Haeger (1960) also found in Florida, that the swarming of male mosquitoes of several genera was highly rhythmical in nature, occurring at dusk and dawn, while mating appeared to occur at any time of the day or night. Nielsen and his co-workers concluded that swarming is a behavioral response to environmental conditions with, as yet, no known function.

Anderson (1974), in reviewing the literature discussing mating phenomena in arthropods, concluded that although much mating may take place at the breeding site and elsewhere, as suggested by Nielsen and his co-workers, a significant number of females of swarming species of mosquitoes are fertilized by swarming males. It is not necessary for all mating to take place in a swarm for swarming to be defined as epigamic behaviour. In a case where the majority of females are mated by males at the emergence site before dispersal, it may be selectively advantageous for the males to continue to make themselves available for mating to any females which left the emergence site before they were mated. In the case of a rapidly

dispersing or migrating population, any female not mated before dispersal begins, would increase her chances of being mated by a male from another population, thus increasing the gene flow between populations separated from one another by time of emergence or location of emergence sites. Swarming may then function as an important form of epigamic behaviour in mosquitoes, a means by which males assemble in a position where they may easily mate with the females of their species.

The stimulus inducing swarming behaviour in mosquitoes is the change in light conditions occurring at sunset and sunrise (Nielsen & Nielsen, 1963). Nielsen and Greve (1950) found that mosquitoes and other biting nematocera in Denmark swarm at approximately the same time each day in relation to twilight and sunset. Nielsen and Nielsen (1953) made similar discoveries with mosquitoes in Florida. Nielsen and Nielsen (1963) concluded that the ability to swarm is always present in males but is only induced by the change in light conditions at twilight, subject to modification by wind, temperature, humidity and other environmental conditions which might limit flight. Some exceptions include Aedes ventro-vittis Dyar which swarm at any time during the day. The stimulus for swarming in this species is not known (Kliwer et al., 1967).

As light intensity and change appear to be important factors in the swarming behaviour of mosquitoes, Nielsen

(1961, 1963) proposed a simple means of measuring the illumination from the sun at twilight. Light intensity is measured in lux, which is the amount of light on a surface receiving 1 lumen per m^2 . A lumen is an expression of light energy output from a source in unit solid angle, measured in terms of its ability to produce a visual stimulus (Nielsen, 1963). However, under standard conditions illumination depends on only the altitude of the sun, which is related to latitude, date, and hour. If one assumes no interference from clouds, trees, haze, etc., then illumination at a specific time can be calculated from the altitude of the sun. Using illumination during twilight and latitude, Nielsen (1963) proposed a unit which could be correlated to this time of sunset or sunrise and the length of twilight. This unit, the Crep (from crepuscular) is described in the Methods.

Values of crep have been plotted against the altitude of the sun and the illumination in ' $\log_{10}\text{lux} + 10$ ' by Nielsen (1963), allowing one to determine the illumination from a clear sky and an unobstructed horizon. $\log_{10}\text{lux} + 10$ is the logarithm of the lux value with the addition of 10 to avoid negative numbers; hereafter this unit will be referred to as "log lux". From Nielsen's charts, $-.88$ crep should have an illumination of $13.35 \log \text{lux}$.

Log lux is used, aside from its convenience, because the sensitivity of the eye is proportional to the

level of illumination to which it is subjected. An increase of 13.40 to 13.50 log lux is the same, to the eye of both man and animals, as the increase from 8.40 to 8.50 log lux, even though the increase in lux is 650 lux in the first case and .0065 lux in the second case. This is the Weber-Fechner's Law (Nielsen, 1963).

Chapter III

MATERIALS AND METHODS

A) Study area

Dispersal studies were conducted over two summers, 1974 and 1975. During 1974, two locations, Pinawa and Sanford, Manitoba were utilized. In 1975 an area near LaSalle, Manitoba served as the mark and recovery site.

Pinawa, Manitoba (Fig. 1) is located in the lower English River section of the Canadian boreal forest, on the western edge of the Whiteshell Provincial Park. This area is characterized by Populus tremuloides Michx Populus balsamifera L. and Picea glauca (Moench) Voss in the well drained areas and numerous swamps and bogs occupied by Picea mariana (Mill) B.S.P. and Larix laricina (DuRoi) K. Koch (Rowe, 1972). Whitetail deer (Odocoileus virginianus) Goldman and Kellog, are common, undoubtedly providing, along with humans, a source of blood for female mosquitoes.

The Pinawa release site was on an island in the Winnipeg River, located near the townsite. Trapping sites for the mark-release experiment were conveniently located along the river and within the townsite (Fig. 1).

The Sanford and LaSalle sites were located in heavily farmed areas of southern Manitoba (Figs. 2 and 3). At Sanford the site was within 30 m of the LaSalle River, and was well treed with Quercus macrocarpa Michx and Ulmus

Figure 1. Map showing trap locations and the release site at Pinawa, 1974.

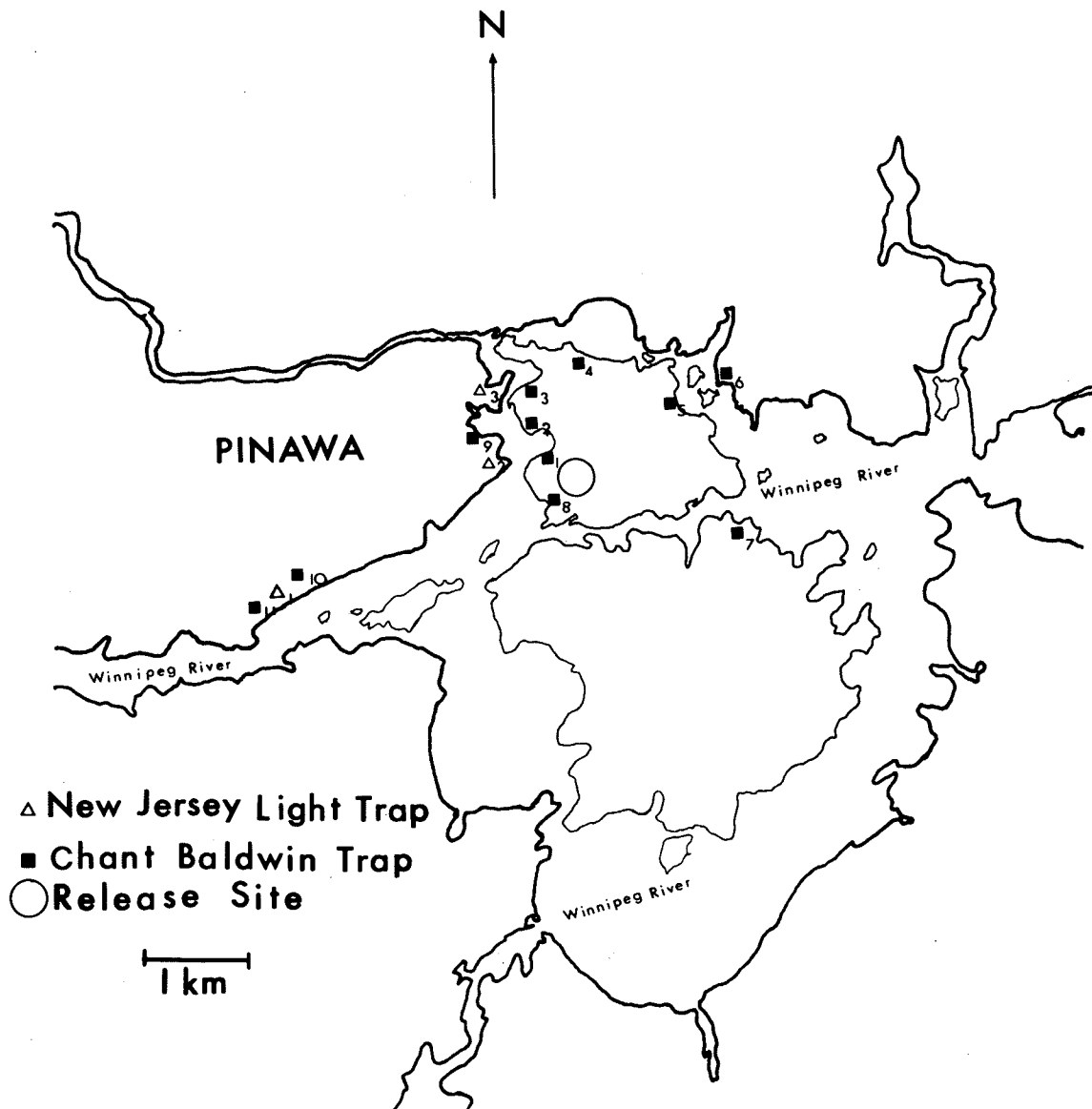


Figure 2. Map showing trapping sites and release site
at Sanford, 1974.

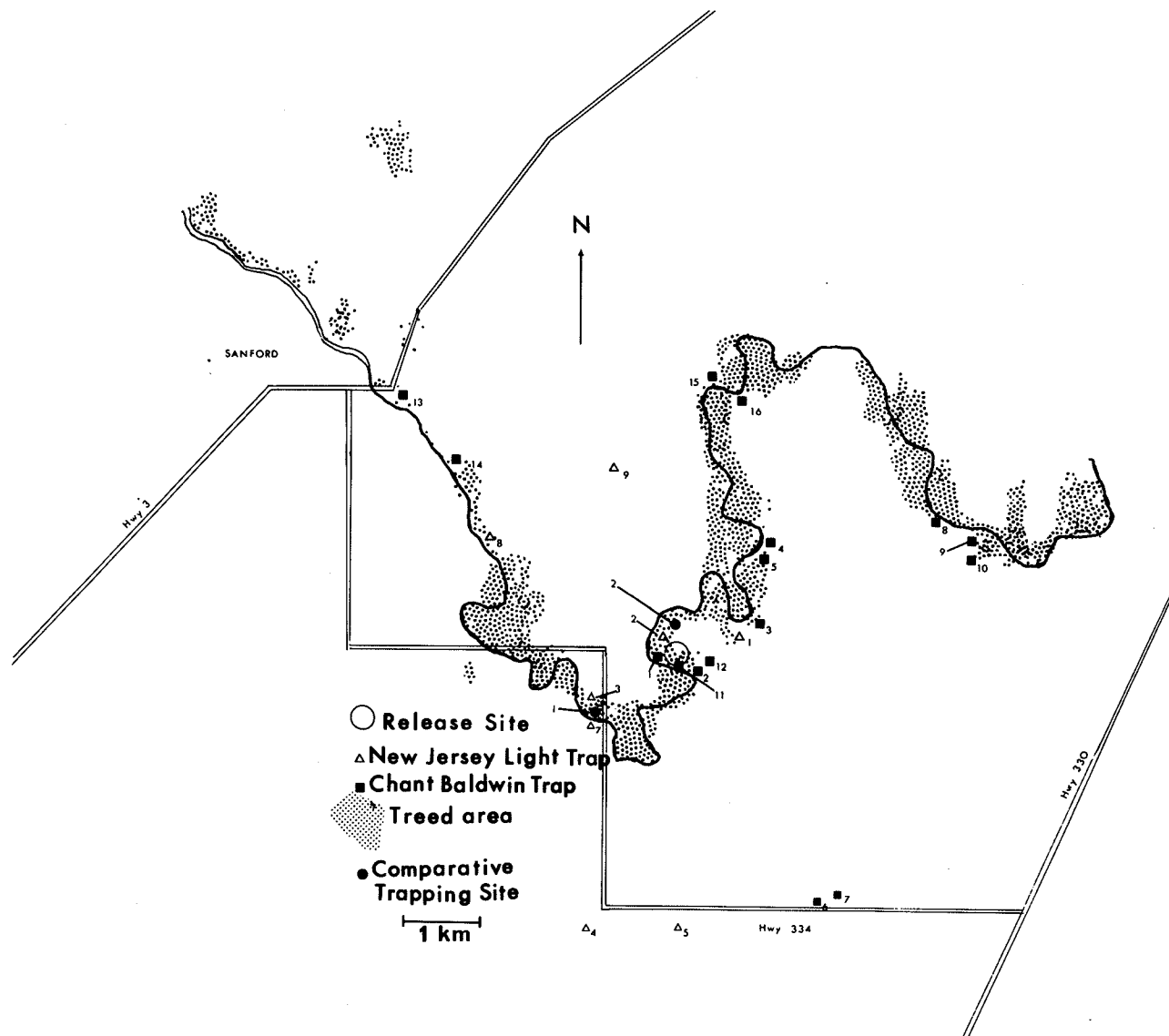
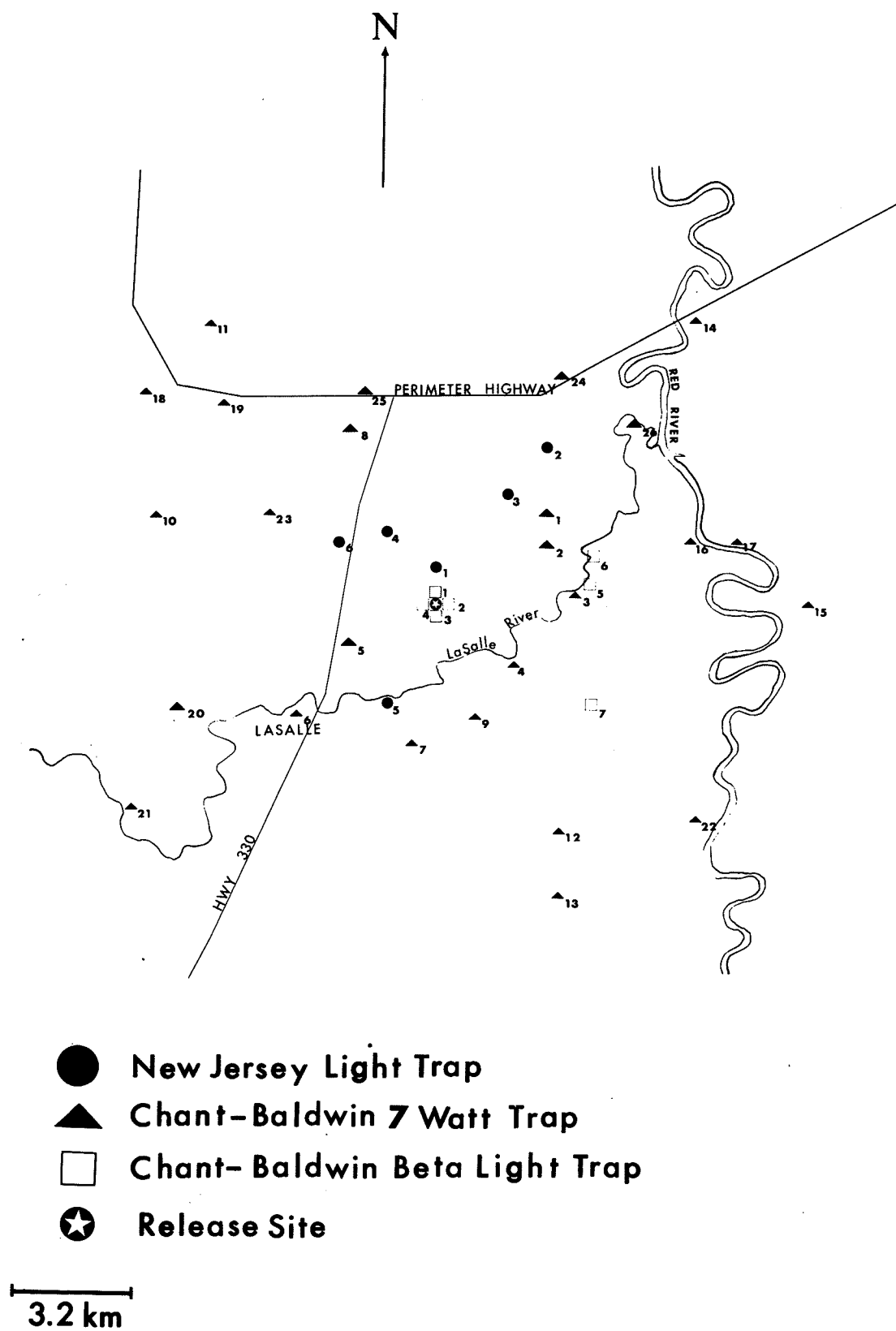


Figure 3. Map showing trapping sites and release site at LaSalle, 1975.



americana L. Prairie grasses as well as field crops were abundant. Cattle occurred in scattered herds throughout the area and humans were present in farm homes and in several townsites.

The LaSalle site was in the same general area of Manitoba as Sanford, and was surrounded by farmlands and with dairy herds abundant in the area. The site was located in an abandoned 1 ha wooded farmyard approximately 4.2 km northeast of the town of LaSalle. This site is 1.9 km northeast of the LaSalle River and 5.8 km south of Winnipeg Perimeter Highway 100. This site was chosen because it provided all the requirements for successful breeding and adult survival and was sufficiently close to the city of Winnipeg to allow an infiltration study into areas where mosquito control is conducted. Environmental conditions in the area, including evening light conditions and prevailing winds, indicated that dispersal could be expected in a northerly direction where it would merge with the areas being sampled by light traps operated by the City of Winnipeg Parks Branch. These traps would extend the recovery trapping area to 39 km north of the R.S. Unlike the 1974 Sanford site, the 1975 LaSalle site did not provide large areas of cover. The closest cover available to dispersing adults was 1 km from the R.S.

A comparison was made of the effectiveness of the trapping methods used. These tests were conducted in two

areas near the 1974 Sanford release site: one a heavily wooded area with a dense deciduous shrub layer and the other in a more open, but treed area with a herb layer of tall grass. The first area was close to human dwellings and the second was near a farmyard with a small herd of cattle.

All observations made on swarming between 5 July and 31 August were made at the 1975 LaSalle release site or within 150 meters of the wooded area of the site. After 31 August, unless otherwise noted, the observation area was moved to a mud roadway 2.5 km south of the 1974 Sanford release site.

B) Collection, marking and recovery methods

The materials used in this study included apparatus for (1) collecting, (2) holding and emergence, (3) marking, (4) recapture, and (5) identification.

Larval mosquitoes were collected using one-litre enamelware dippers to remove mosquitoes from snow-melt or rain filled pools. Collecting was aided when larvae displayed "balling behaviour" in which large aggregates of 4th instar larvae gathered together, or in areas where breeding sites had decreased enough in size to concentrate the larvae for easy collection. When concentrations of the larvae were not available, they were concentrated by using a soil sieve with a 0.5-1 mm mesh. The larvae collected were temporarily held in 20 l plastic buckets and then transported by hand or truck to plastic lined rearing and

emergence pools and boxes.

At Pinawa, the larvae were first placed in holding pools constructed by stretching 6 mil. polyethylene plastic over a crude frame of logs. In these pools, the larvae were reared on a diet of ground dog food, as well as leaf litter and debris collected along with the larvae.

In other studies, larvae were placed directly into the 1 m² emergence boxes made from wooden frames lined with plastic and filled one-half to two-thirds with water. Over each emergence pool a pyramidal cage having a wooden frame and screen covering was placed to capture newly emerged adults (Briand, 1974).

Marking of mosquitoes was accomplished by the use of dyes in 1974 and a radioactive isotope in 1975. Dyes used at Pinawa and Sanford were Rhodomin B and Fast Green, dissolved in 95% ethanol as recommended by Edman and Lea (1972). Slightly less than a saturated solution was used. These dyes were delivered in a fine mist from a hand-held compressed air sprayer. When a sufficient number of mosquitoes had emerged (200-1000 per cage), the cages were removed from the pools and placed on a patch of dry grass. The dye-ETOH solution was applied through the screen and the wet adults were allowed to drop to the grass where they dried and flew away at will. Spraying occurred in the evening or early morning when humidity was high and local winds low. If winds were high at the evening marking

period, marking was postponed up to 24 hours until atmospheric conditions were more favorable. At Pinawa, an estimated 36,000 adults (75% Ae. communis and 25% Aedes trichurus (Dyar)) were marked. At Sanford, 175,000 Ae. vexans were marked. These estimates were made by random samplings of known amounts of pool water.

Radioactive marking was accomplished using the phosphorus isotope ^{32}P . Laboratory tests were conducted to determine the levels of radioactivity that could be used to mark mosquitoes effectively. For our purpose adults would have to have sufficient radioactivity so that the marked adults could be identified up to 30 or 40 days after release. To determine the amount of ^{32}P needed, late 3rd and early 4th instar larvae of Ae. aegypti were placed in pans containing 10, 1.0 and 0.1 $\mu\text{Ci/l}$ ^{32}P and liver powder as food. After pupation, the mosquitoes were removed and placed in cages; after emergence the adults were given water and sucrose. After pre-determined periods of time, the adults were killed and tested for radioactivity in a low energy Beta Counter. Adult Ae. vexans reared under similar conditions were also tested for the level of radioactivity 30 days post treatment.

Other tests were conducted to determine the lowest rates of radioactivity which would identify marked mosquitoes when they were exposed to prepacked medical x-ray film.

For field marking with ^{32}P , the equipment was basically similar to that used for dye, except that emergence pools were made stronger, using two layers of plastic sheeting. The ground under the pools was cleared to remove any sharp objects that would pierce the plastic and pyramidal cages were placed on the pools at all times to prevent stray animals from drinking the radioactive water. ^{32}P was added to each of 17 pools to make the final concentration $0.1 \mu\text{Ci/l}$ before larvae were placed into the water. Safety films were worn by all persons visiting the R.S.

The first dispersal experiment in 1975 was conducted with Ae. vexans collected from Brandon, Manitoba. On 17-19 June, 200,000 1st and 2nd instar larvae were transported by truck to LaSalle and placed in the radioactive pools. Heavy rains on 22 and 23 June, however, caused most of the pools to overflow and this resulted in the loss of a large number of larvae from the pools. During the heavy rain an egg hatch of Ae. vexans occurred at the R.S. and the collections from this population were added to the pools. ^{32}P was added to the pools to bring the concentration back to an estimated $0.1 \mu\text{Ci/l}$. An effort was made to collect all the larvae before they reached the 3rd instar, but poor weather and bad road conditions made collection difficult. As a result, most of the larvae were collected as 4th instars. The emergence of the two populations (LaSalle and Brandon) overlapped,

occurring over the period 20 June to 4 July. The largest number of adults emerged on 1-2 July (250,000) and a total of 300,000-310,000 marked Ae. vexans adults were released. July 1 was considered day one for recapture records. The radioactivity of these newly emerged adults was checked in a low energy Beta Counter.

Five methods were utilized to capture marked adults in 1974 and 1975; sweeping with a hand net in grass and bush, standard New Jersey light traps (N.J.L.T.) and three modifications of the CO₂-light trap (C-B trap) developed by Chant and Baldwin (1972).

Sweeping was conducted primarily at the release site to capture marked adult females to determine when insemination occurs and the time that the majority of females leave the emergence site.

Standard New Jersey Light Traps (N.J.L.T.) operated with 60 watt incandescent bulbs were used in all three dispersal experiments. At Pinawa three were operated, in locations around the townsite. At Sanford, nine, and at LaSalle, six were operated. At both LaSalle and Sanford, N.J.L.T.'s were operated in suitable locations with 110 watt electrical power. At LaSalle, two traps were operated in close proximity to cattle feedlots; three were located on farmyards with no animal herds, and one was operated in a wooded area approximately 200 m from a field containing a small beef cattle herd. Records were kept of the trap collections so that the various types of locations could be compared.

The CO₂-Light traps used were all modifications of the battery-dry ice trap designed by Chant and Baldwin (1972). The first modification, suggested by Chant and Baldwin but not part of their standard design, consisted of placing the battery operated light above the cone screen. This was found by Chant and Baldwin to attract a larger number of mosquitoes. Twelve of these Chant-Baldwin (C-B battery) traps were operated at Pinawa and 16 at Sanford. A second modification of the C-B trap was made by replacing the battery operated light with a clear 7 watt bulb powered by a standard 110 volt electric outlet. Twenty-six of these Chant-Baldwin CO₂-7 watt light traps (C-B 7 watt) were operated at LaSalle. The third modification was made by replacing the battery operated light by a radioactive Beta light (Tritium) source (C-B_β) as suggested by Baldwin and Chant (1975). These traps were operated in areas where no electricity was available, and eight were utilized in the LaSalle study. Baldwin and Chant (1975) showed these traps to be as effective as battery operated traps in capturing adult mosquitoes. (Table 1).

All three C-B trap types were baited with dry ice and their power source connected each night. Small strips of vaponal¹ in the N.J.L.T.'s assured that all captive insects were dead by morning. Insects in the C-B type traps were incapacitated by spraying them with ether or a

¹Dichlorvos

Table 1. Number of adult female mosquitoes captured in 1972 and 1973 in a beta light and 3 battery operated traps (after Chant and Baldwin, 1975)

	Battery operated traps				Beta light trap
	1	2	3	mean	
1973	915	2735	1068	1537	1740
1974	806	1611	1160	1192	1154

solution of pyrethrin in 95% ethanol. Mosquitoes taken in N.J.L.T.'s had to be separated from other insects. Little or no separation was required with any C-B trap. In 1975, a record was kept of the time required to prepare catches for identification in order to determine the work-time advantage of each trap type.

A comparison was made in 1975 of the effectiveness of the trapping methods used. N.J.L.T.'s, C-B battery, C-B -7 watt, C-B with no light source, and two sweeping techniques were tested. The two sweeping techniques used were sweeping the air around the collector and around several blocks of dry ice (air sweeping), and sweeping in grass and brush (grass sweeping) for resting adults. A CO₂ bait trap designed by Trimble and Thorsteinson (1974) was also evaluated.

Marked adults were identified by various methods. Dye marked adults were identified by placing all the captured mosquitoes on white paper towels and dropping 95% ethanol on each individual insect. Marked adults were recognized by the spot of dye left on the paper towels. In 1975, all captured mosquitoes were exposed to medical x-ray film, either prepacked or in cassettes. Marked mosquitoes were recognized by the shadow produced on the film.

C) Swarming

The procedure involved in studying swarming included recording the location of swarms, sampling of swarms, preserving, mounting and identification of collections. Swarms occurring as flying groups of adult mosquitoes above roadways, bushes and other objects, were located by sight. Sampling was done with a sweep-net and the collected specimens removed with an aspirator and placed in vials of 70% ethanol. Temperature and humidity were determined with a thermometer and a sling psychrometer; cloud cover, wind direction and wind speed were recorded as often as possible. Time of day was also recorded for each collection so that it could be transposed into crep units. In the laboratory, mosquitoes were identified with the aid of a dissecting microscope. Males of Ae. vexans were removed and counted. Other males were identified by mounting the terminalia in glycerin or Canada balsam after the appropriate processing. Identification was then made with the aid of a compound microscope.

Time of day was changed into crep units as proposed by Nielsen (1961, 1963) as a means of standardizing the time with sunset and length of twilight. Crep units were calculated in the following manner:

$$\frac{\text{Time of day} - \text{Time of sunset}}{\text{Duration of twilight}} - \text{for evening}$$

or

$$\frac{\text{Time of sunrise} - \text{Time of day}}{\text{Duration of twilight}} - \text{for morning}$$

The time of sunset (or sunrise) and the length of twilight varied with the date and the geographical location. In Winnipeg on 11 July, 1975, the sun sets at 20 08 standard time (Percy, 1975), and twilight lasts 42 minutes (Beck, 1968). Therefore, in crep units 20 00 is -0.19 crep and 20 40 is 0.76 crep.

Chapter IV

RESULTS

A) Dispersal studies1) Pinawa

During this study, 36,000 marked adults (75% Ae. communis, 25% Ae. trichuris) were marked using fast green or rhodamin-B dye. The marked adults were released between 27 May and 3 June, with the majority being released on 3 June (21,000). Recoveries were made by sweeping within a few metres of the release site and by the use of C-B battery traps. The three N.J.L.T.'s operated across the Winnipeg River (Fig. 1) in the townsite captured no marked adults. Thirty-nine marked mosquitoes were captured (.1% of the release), 37 by sweeping at the R.S. Captures by sweeping were made between 31 May and 11 June, 1974. One marked adult was recovered in a C-B battery operated trap on 10 June, at the R.S. Another marked recovery was made on 12 June, 1.1 km from the R.S. All recovered adults were Ae. communis. Table 2 summarizes the Pinawa recoveries.

2) Sanford

At Sanford, 175,000 adult Ae. vexans were marked and released over a period of seven days (4 June - 12 June, 1974). The majority of these mosquitoes were released on the 5th, 6th and 7th of June. June 6th is considered the

Table 2. Recovery of marked Aedes communis at Pinawa, 1975

Date	Site	Distance from R.S. in km	Methods of recovery	Number of marked mosquitoes recovered	Mated
31/5	Release site	0	sweeping	29	no
3/6	Release site	0	sweeping	1	no
4/6	Release site	0	sweeping	1	no
5/6	Release site	0	sweeping	4	no
6/6	Release site	0	sweeping	1	no
10/6	Site #2	.21	C-B	1	no
11/6	Release site	0	sweeping	1	yes
12/6	Site #5	1.1	C-B	1	yes

mean release day and 7 June is day one of recovery. A total of 178 marked adults were recaptured (.102% of total release); 161 of these by sweeping (127 females, 34 males) in the immediate vicinity of the R.S. (Table 3). Sweeping was conducted up to 13 days after release.

Twenty-five traps were used in this study, nine N.J.L.T.'s and 16 C-B battery traps. Seventeen marked Ae. vexans females were recovered from these traps, up to 32 days after release and 3.9 km from the R.S. (Table 4). Most (14) of these mosquitoes were from traps within .5 km of the R.S. N.J.L.T. #2 recovered the majority of marked adults (9).

3) LaSalle

A total of 300,000-310,000 marked Ae. vexans were released in the LaSalle study. The emergence of radioactively marked adults lasted from 20 June - 4 July 1975 with the bulk of adults emerging on 1-2 July (250,000). July 1 is considered day one for recapture records. Samples of newly emerged adults were evaluated in a low energy beta counter (Table 5) and showed levels of radioactivity lower than had been expected. Laboratory studies had led the investigator to expect beta counts of 400-500 cpm, which would have been sufficient to detect marked adults through 2 half lives of 14.3 days.

Marked adults were recovered via three different collection methods; sweeping, N.J.L.T. and C-B 7 watt traps

Table 3. Marked female Aedes vexans collected by sweeping within 0.2 km of the Sanford release site

Date	Number of marked females recovered	Mated	Number of days after release
8/6	21	no	2
9/6	89	no	3
10/6	8	no	4
12/6	3	no	6
14/6	4	2-yes, 2-no	8
17/6	2	yes	11



Table 4. Marked female Aedes vexans collected by trapping within a 4 km radius of the release site at Sanford

Date	Site	Number of marked mosquitoes recovered	Distance from release site (km)	Days after release
6/6	C-B #6	1	3.9	1
14/6	C-B #2	1	0.3	8
	C-B #12	1	0.5	
	N.J.L.T.#7	1	1.1	
	N.J.L.T.#2	6	0.3	
19/6	N.J.L.T.#3	1	0.3	13
20/6	N.J.L.T.#2	1	0.3	14
	C-B #1	1	0.0	
	C-B #12	1	0.3	
21/6	N.J.L.T.#2	1	0.3	15
4/7	C-B #15	1	3.5	28
8/7	N.J.L.T.#2	1	0.3	32

Table 5. Radioactivity of marked Aedes vexans at time of release at LaSalle, Manitoba, 30 June-2 July, 1975

Date	Number of mosquitoes tested	Range C.P.M.	Average C.P.M.
30 June	11	13-61	21
1 July	15	12-195	61
2 July	20	26-97	51

(Table 6). No marked adults were captured in C-B traps. Six marked adults were recovered by sweeping at the R.S. (Table 6). Two males and three females were captured on 30 June and one female was captured on 1 July. No ^{32}P -marked recoveries were made after 1 July at the R.S. C-B 7 watt traps captured 3 marked females, 2 from trap #8 (Fig. 4), 5.5 km from the R.S.; one was taken 14 days and the other 16 days after release. C-B 7 watt trap #8 captured 12% of the total mosquitoes taken in C-B 7 watt traps. The third recapture from a C-B 7 watt trap was made on 16 July, 15 days after the release (trap #16) and 6.7 km from the R.S. Trap #16 trapped 3.6% of all captures by C-B 7 watt traps. N.J.L.T.'s captured 10 of the 20 marked adults taken in 1975. Of these marked recoveries, 9 of the 10 were recaptured in the two traps which captured over 90% of the adult mosquitoes taken in N.J.L.T.'s. These two traps, #4 located 2.2 km from the R.S. (Fig. 4) which captured 7 marked adults, all 6 days after release and #1 (Fig. 4) 1 km from the R.S. which captured 2 marked adults 15 days after release, were located near cattle feed lots.

B) Insemination of marked females

At Pinawa, all recovered adult Ae. communis females were dissected to determine if insemination had occurred. Twenty-nine females recovered on 31 May were not inseminated. Females recovered from 3 June (last day of marking) to 10 June were also not inseminated, but three marked adults

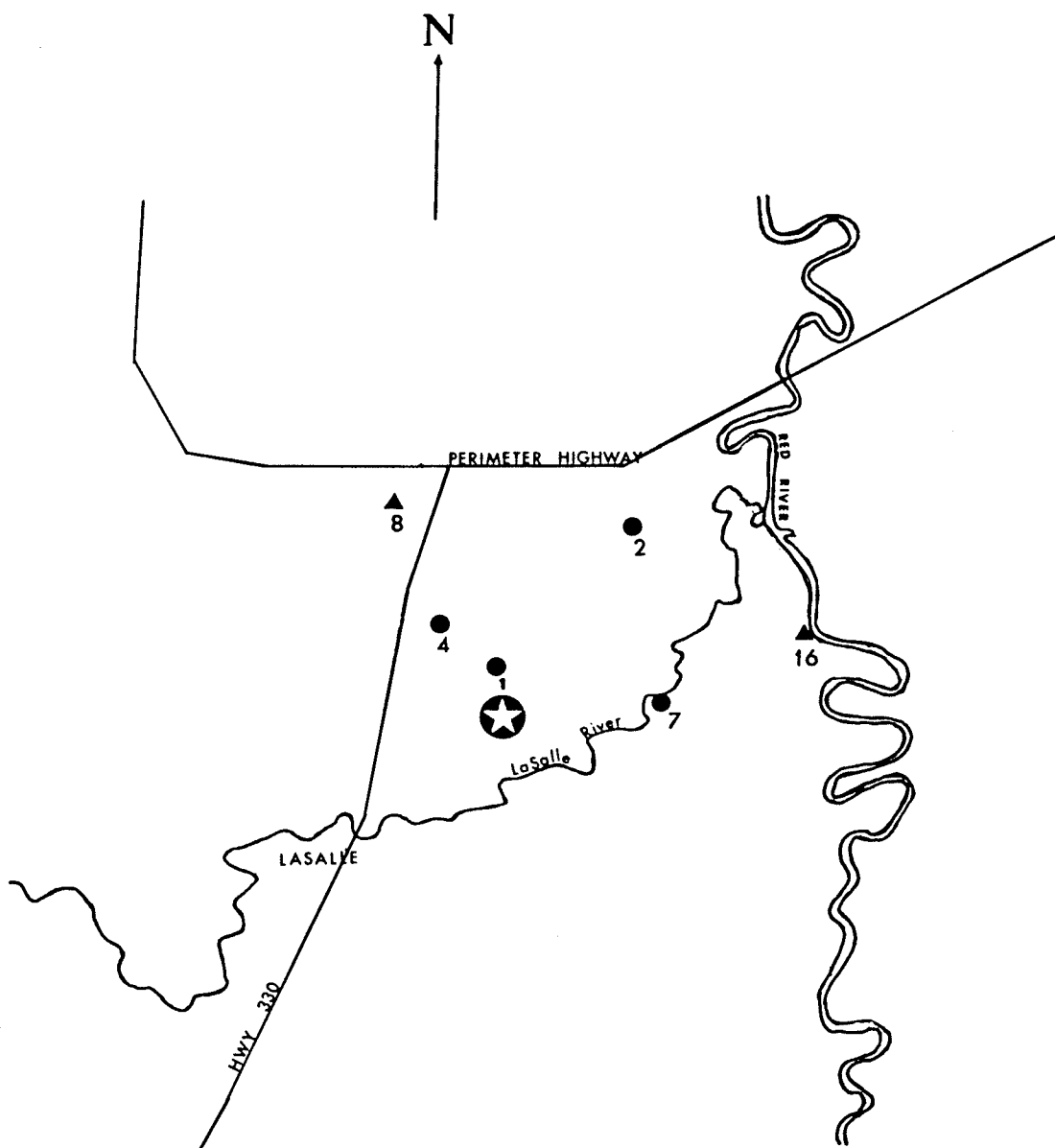
Table 6. Summary of recovery results at LaSalle in 1975

Date	Distance from R.S. (a) in km	Time (days)	Collection method	# Marked recovered
30 June	0	-	Sweep	5
1 July	0	-	Sweep	1
2 July	5.2	1	N.J.L.T.#2	1
7 July	2.3	6	N.J.L.T.#4	7
7 July	18.0	6	N.J.L.T.#7 ^(b)	1
15 July	5.5	14	C-B 7 watt #8	1
16 July	1.0	15	N.J.L.T.#1	2
16 July	6.8	15	C-B 7 watt #16	1
17 July	5.5	16	C-B 7 watt #8	1

(a) Release site

(b) N.J.L.T. #7 operated by City of Winnipeg Parks Branch

Figure 4. Map showing location of traps which recovered marked adults in 1975 at LaSalle.



● New Jersey Light Trap
▲ Chant-Baldwin 7 Watt Trap

★ Release Site

3.2 km

taken after 10 June were inseminated (Table 2).

All 127 marked Ae. vexans females captured by sweeping at the Sanford R.S. were dissected to determine insemination. From 8 June until 12 June, none of the recovered females were mated. On 14 June, two of the four marked females captured were inseminated and from 17 June on, all captured marked females were mated. Males were also recovered by sweeping at the R.S., however, marked males disappeared from the R.S. 2 days before mated females began to appear (Table 3).

In 1975 at LaSalle, the use of radioactively marked adults made it difficult to determine in a short time if an adult was marked or not. However, the results of a general sweeping and dissecting of individuals in samples obtained indicated that female Ae. vexans were inseminated by 4 days after emergence.

C) Comparative trapping techniques

In the comparative trapping study conducted at Sanford, the N.J.L.T.'s and C-B 7 watt traps recovered the largest number of adult females. In site one, (Table 7) (Fig. 2), the heavily treed area, the C-B 7 watt trap averaged 85.6 females per night and the N.J.L.T. averaged 57.6 per night. More than twenty adult females per night were also recorded in air sweeping and C-B battery trap. The C-B 7 watt trap was 3.9 times more effective than the battery operated C-B trap.

TABLE 7. Number of female mosquitoes collected using different trapping techniques at Sanford, Manitoba

Date	Standard N.J.L.T.		C-B battery trap		CO ₂ bait trap (c)		C-B 7 watt trap		C-B trap (no light)		Grass sweeping		Air sweeping	
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
3/7	149	69	5	55	4	0	91	44	--	--	47	0	86	27
7/7	---	50	---	--	--	--	--	--	--	--	--	--	--	--
10/7	58	156	150	--	0	4	354	54	--	12	20	0	119	1
12/7	25	158	8	26	10	18	246	117	6	16	12	0	4	0
16/7	89	51	1	20	21	3	68	29	1	3	5	7	8	5
18/7	51	32	1	6	3	1	15	4	0	0	1	3	7	9
19/7	46	45	5	1	1	0	73	11	0	0	13	4	13	8
22/7	20	--	--	--	--	--	--	--	--	0	--	--	--	--
23/7	--	24	--	21	--	4	27	26	--	1	4	--	5	--
24/7	--	27	11	4	2	1	6	8	1	--	3	--	22	--
25/7	40	40	7	0	6	0	14	35	0	--	--	--	--	--
30/7	26	--	--	--	--	--	22	--	--	--	--	--	--	--
31/7	36	259	11	22	2	9	26	358	--	7	3	9	8	6
Average	58.6	78.4	22.1	18.0	5.4	4.0	85.6	68.6	1.3	5.4	12.0	3.3	30.2	8.0

(a) Site 1, heavily wooded with deciduous shrub layer.

(b) Site 2, lightly wooded with herb layer of grass.

(c) Trimble and Thorsteinson (1974)

In site two, (Table 7) (Fig. 2), with less vegetation, the N.J.L.T. (78.4 females per night) was more effective than the C-B 7 watt trap (68.6 females per night). In area two, none of the other methods used captured more than an average of 20 adult females per night. The C-B 7 watt trap was found to be 3.8 times more effective than the C-B battery operated trap.

Records were also kept of the success in capturing all mosquitoes as well as marked adults in each of the 40 traps operated around LaSalle. These were compared with respect to the local conditions at each site.

The twenty-six C-B 7 watt traps used at LaSalle were operated for a combined total of 489 trap nights in 1975. Traps were operated four nights a week. A total of 155,380 adults were captured (average = 318/trap/night). In July, the traps were operated a total of 310 trap nights and captured 144,823 adults (467/trap/night). The adult mosquitoes collected were distributed amongst the 26 traps in the following proportion: 50% in 6 of the traps, 75% in 12 traps and 90% in 19 traps. The 6 traps which captured 50% of the mosquitoes, consistently captured the majority of adults each night. The 8 C-B_B traps averaged 98 captured adult mosquitoes per night. C-B 7 watt traps captured 3 marked adults; 2 in the trap which captured 12% of the adults taken, the largest part of the capture, while the third marked capture was from a trap which collected 3.6% of the total catch.

The six N.J.L.T.'s captured 164,000 adult mosquitoes in 329 trap nights (average = 498/trap/night). During July, on the same nights that the C-B 7 watt traps were operated, the N.J.L.T.'s captured 65,607 adults in 62 trap nights (average = 1058/trap/night). The number of adult mosquitoes captured in N.J.L.T.'s was not evenly distributed, 90% of all adults were captured in only two traps. The two traps, #4 and #1 (Fig. 4), were both located near cattle feed lots. Trap #4 (80% of captures) was within a few feet of a feed lot. The recovery of marked adults closely follows this pattern, with 9 of 11 marked recoveries from N.J.L.T.'s being taken in trap #4 (7 recoveries) and #1 (2 recoveries).

Records were kept during 1975 of the length of time necessary to process trap catches from N.J.L.T.'s and C-B traps. The amount of time required to sort adult mosquitoes from the other insects in a trap catch was recorded by each student involved and recorded in Table 8. C-B CO₂ traps required less time and manpower in the laboratory but more time and manpower in the field.

D) Observations on the swarming of male *Ae. vexans*

Swarming male *Ae. vexans* were collected in 30 samples (Table 9). Some were collected each night that swarms were observed. The first observation of a marker swarm was made shortly after sunset on 5 July. This swarm (not shown in Table 9) consisted of a spiral shaped mass over a small car parked on the dirt roadway near the 1975

Table 8. Processing times for trap collections

Student	CO ₂ traps		N.J.L.T.'s	
	Number of mosquitoes per minute	Number of trap collections processed	Number of mosquitoes per minute	Number of trap collections processed
1	6.74	53	2.95	23
2	7.2	87	5.33	21
3	7.0	79	4.79	15
4	6.43	24	4.09	21

LaSalle release site. It was estimated that this swarm consisted of between 3-6 thousand individuals and started about 1.7 m above the ground (.2 m above the top of the car) reaching to about 4 or 5 m above the ground. All the individuals in this swarm faced into a wind of about 10 km/h and toward the setting sun. The individual members of the swarm moved about in a darting manner, largely backwards and forwards, but often vertically in the swarm, giving the swarm a pulsating appearance. A sample of 96 from this swarm indicated that 90% were Ae. vexans males.

Ae. vexans males were often observed swarming with other males as well as female mosquitoes. Female mosquitoes were present in almost all samples from swarms. It was not possible to determine if these females were part of the mass of blood seeking adults always following an observer about, or if they were taking part in the swarm. In all cases, except where noted, females are included as part of the swarm. Chironomids and other dipteran males were present in 47% of the samples taken and made up between 2% to 99% of the individuals present.

Culex restuans Theobald males were also present in swarms with Ae. vexans, ranging from 88% of the sample to as low as 6% of the sample and were present in 22% of all samples with male Ae. vexans. Cx. restuans was the most frequent male in three of the samples containing Ae. vexans males. Cx. tarsalis males were present in 6 samples; 4 of these also contained Ae. vexans males.

Aedes spencerii (Theobald) males were also present in three of the swarms containing Ae. vexans males (Table 9). It should be noted that the males of Ae. spencerii and Ae. sticticus are difficult to differentiate. It is assumed that the species observed is Ae. spencerii as it fits this determination best. Other species of male mosquitoes present in the area were taken in sweep samples in nearby bushes, but were never taken in samples from swarms. These are listed in Table 10.

Swarms of Ae. vexans ranged in size from single males to 5 or 6 thousand individuals. Top swarms were small, with relatively few Ae. vexans males and only small samples could be taken (Table 9). Marker swarms were larger and contained greater numbers of Ae. vexans, proportionally, and numerically than did top swarms.

1) Top Swarms

Seven top swarms were observed, which had formed near the lee side of bushes and other vertical objects. Many more were seen during the study period but these were not sampled. Of the seven swarms sampled, 5 contained different numbers of male Ae. vexans, ranging from 3% of a sample of 31 (0.10 crep on 11 July) to 100% of the male mosquitoes sampled in a small swarm of about 25 individuals at -0.86 crep on 11 July (Table 9). In the total swarms sampled, Ae. vexans made up only a small component of the individuals present. Female mosquitoes made up the

Table 10. Males of other species found at release site.
These were not captured in any of the swarms
sampled.

Culiseta inornata (Williston)

Aedes excrucians (Walker)

Aedes canadensis (Theobald)

Aedes riparius Dyar and Knab

Aedes trivittatus (Coquillett)

Aedes dorsalis (Meigen)

largest single component, being present in all 7 samples and averaging 38%.

Other dipteran males made up the second largest component, being present in 5 samples and averaging 21% (29% in the 5 in which they were present). Ae. vexans made up the smallest component, being found in 5 of the 7 samples. It made up 8% of the 5 samples in which it was present. Ae. spencerii and Cx. tarsalis were taken in 3 of the seven samples and each averaged 21% in these samples.

2) Marker Swarms

a) Marker swarms formed over a roadway. Marker swarms over a roadway or some other visual contrast marker were observed on 10 evenings and 29 samples were taken. Five of these swarms formed over mud roadways, one over the edge of a newly cut grain field, and 4 over unidentified markers either in a ditch or on a roadside. These last 4 may be free swarms as described by Nielsen and Haeger (1960). Another variation of the marker swarm occurred when adult mosquitoes gathered above an automobile or other object protruding from the surface of a roadway. This form occurred on 9 evenings and 19 samples were taken.

The swarm marker of mosquitoes over roadways appeared to be the contrast between the green or light brown of the roadside and the dark grey mud of the road itself.

In the study area, the roadway had a centre strip of grass. The roadway was also raised 0.5-1 m above the surrounding fields and was separated from the fields by ditches on both sides. The ditches were 1-2 m deep and approximately 3.5 m wide.

i) LaSalle site. Marker swarms that formed over roadways tended to be in the form of a sphere between 2-2.5 m above the ground and .5-1 m across. The first swarm of this type was observed at 0.95 crep on 9 July over the roadway immediately to the east of the 1975 LaSalle R.S. Several swarms were observed at approximately 50 m intervals along the roadway. All swarm members faced northwest, into the wind and the setting sun. A sample from one of these swarms proved to be 70% male Ae. vexans (Table 9). By 1.4 crep these swarms had dissipated, but scattered individual males hovered along the roadway in what appeared to be a continuation of the swarming behaviour.

On 11 July, at 1.29 crep, a swarm of several hundred individuals was sampled over the roadway. This swarm was 2.4-3 m above the ground and spherical in shape. Ae. vexans males made up the majority of a sample of 22 (Table 9). A very small swarm of 40-50 individuals which was sampled on 13 August at 0.42 crep, proved to be 80% Ae. vexans males (Table 9). On 31 August, at 0.38 crep, a large swarm was sampled and found to contain less than 1% Ae. vexans (Table 9).

At 0.69 crep on 11 July, a swarm of several hundred individuals was sampled along a tractor track leading into an alfalfa field, approximately 100 m north of a 1 ha stand of oak at the 1975 LaSalle release site. A sample was 40% Ae. vexans males (Table 9). One small swarm observed on 11 July at 0.36 crep, formed over the west side of the ditch on the west side of the road at the release site. This swarm, a ball about 0.3 m in diameter and 1.7 m above the ground was not formed over any recognizable swarm marker. The ground below this swarm was a complex of shadows and tufts of grass, none of which could be seen as an obvious marker, indicating that this could be a "free swarm" as defined by Nielsen and Haeger (1960). Ae. vexans males comprised one half of a sample from this swarm, with chironomids and female mosquitoes comprising the other half (Table 9).

ii) Sanford site. On 4 September, another swarming site was found on a dirt road running into a field of cut and swathed grain located 2.6 km southeast of the 1974 Sanford R.S. This area was similar to the previously discussed swarming site, but lacked a stand of trees. There was a 10 m wide culvert leading across the ditch separating the dirt road from the field. The skyline, 3.2 km to the north and 4.8 km to the west, was lined by trees growing along the LaSalle River. These trees obscured the sun at sunset before it passed below the horizon. On all other

sides the horizon could be observed. Ae. vexans males swarmed at two locations over visual contrast markers at this second site, both locations over parts of the culvert separating the road from the field. The first site, 1.5-2 m in from the road, was an area with no distinct swarm marker, but a network of shadows and tufts of grass covered the ground below the swarms. Three swarms were observed over this point. The second site, approximately 5 m from the first, was over the edge of cut grain where mature standing grass about 1 m high contrasted with the recently cut stubble of the grain field. Swarming was observed only once over this point.

On 4 September at 0.50 crep, a swarm of 500-1000 individuals was sampled over the first location mentioned above. This swarm, a compact ball, was 1.5-2.5 m above the ground and 1-1.2 m across. In a sample of 54 individuals, all were male Ae. vexans. On 14 September, at -.03 crep, a lone male Ae. vexans was collected over this site, approximately 2 m above the ground. At .12 crep, a number of males observed rising from the grass at this location, during periods of low wind velocity were all Ae. vexans (Table 9). At 0.64 crep, a small swarm of 100-200 individuals, 1.5-2.5 m above the ground, proved to be all Ae. vexans males.

One sample taken at the site over the edge of the cut grain, was taken at 0.50 crep on 4 September. This

swarm of 4-5,000 individuals was 98% Ae. vexans males (Table 9). The swarm was 1.5-2.5 m above the ground and 0.6-1 m across.

One other swarm was observed, about 2.6 km directly south of the above mentioned site and 5 km south of the Sanford release site. This swarm, observed on 13 September over a gravel road with deep ditches on either side (4.5 m deep on the south side and 2.5 m deep on the north) was observed directly after sunset. About 50 individuals participated in the swarm and one coupling pair, collected by hand, appeared to be Ae. vexans.

b) Marker swarms formed over an object protruding from a roadway. A variation of the marker swarm occurred when swarms, usually larger than the other marker swarms, formed over an automobile or the head of an observer standing on a roadway. It is believed that these swarms were first attracted to the visual contrast of the roadway and secondly to the presence of a large object protruding from the road. When an observer moved beneath one of the marker swarms on a roadway, and moved along slowly, the swarm remained above the observers head. Other swarms contacted along the roadway joined the former one and a swarm of 1000 individuals formed in this manner. These mosquitoes remained with the observer as long as he moved upwind slowly, or downwind. If the observer ran upwind, the swarm was left behind.

Marker swarms which formed over objects protruding from roadways differed from top swarms in that they always formed directly over an object while top swarms usually formed to the lee side of an object.

The marker swarms which formed over an object were observed on 9 evenings. Out of 19 samples, 14 were from swarms which formed over a car or truck. Swarms of this type were generally first noticed when a few scattered males hovered over the cab of a truck or the tallest part of a car. The number of individuals grew until a sphere was formed of several hundred individuals, 1.5-3.0 m above the ground and .5-1.5 m above the top of the marker. On several evenings, this sphere continued to grow until a tall spiral, 1.5-5.5 m above the ground (0.5-3.6 m above the top of the marker) was formed. These swarms were as wide as the top of the marker and formed a loose spiral up to their peaks.

i) LaSalle site. The first of these swarms was noticed on 5 July over a small truck parked on the roadway immediately east of the LaSalle R.S. The swarms on this evening and on 6 and 11 July were tall spirals up to 4.9-5.5 m above the ground, and contained an estimated 4-6 thousand individuals, largely Ae. vexans males. It is not known when the swarms began on 5 or 6 July, but on 7 July, a swarm began to form over an automobile at 1.36 crep and lasted until 1.69 crep. Gusty winds occurred on the evening

of July 7 until shortly before 21 24 (1.0 crep). Swarming did not begin until after the wind had slowed. All males in a sample of 63 were Ae. vexans.

The first indication of swarming over a small truck on 9 July appeared at 0.07 crep. A sample of 16 was 63% Ae. vexans males (Table 9). By 1.0 crep the main body of the swarm had shifted to directly above the flat bed of the truck, to the lee side of the cab (1 m above the ground) and contained between 2-3 thousand individuals. A sample of 29 proved to be only 7% Ae. vexans (Table 9). The location of this swarm, to the lee side of the truck cab, would indicate that it was only partly a mating swarm and was mostly a large aggregation of females perhaps seeking shelter from the wind. On 11 July, a cool evening with a light wind, a small swarm of from 50-100 individuals began to form at -0.14 crep over a small truck. This swarm was found to contain 6% Ae. vexans males (Table 9). By 0.21 crep, the proportion of Ae. vexans males had grown to 30%. However, when this swarm was next sampled at 1.45 crep, it had grown to about 1000 individuals and contained only 4% Ae. vexans males (Table 9). By 1.76 crep, this swarm contained less than 25 individuals. A sample of 8 contained no Ae. vexans males (Table 9).

On 15 July, a warm windy evening, the first occurrence of swarming activity began at 0.14 crep. This swarm, approximately 9 meters above the ground at its lowest point,

could not be sampled. The swarm appeared to extend well above the 9 metre level, but because of the lighting conditions at the site, the total height of the swarm could not be determined. At 0.52 crep, a small swarm had formed over the cab of a small truck but contained no Ae. vexans males (Table 9). However, by 1.0 crep, a small swarm formed over the head of the observer standing directly by the truck. Sampling from this swarm revealed 80% Ae. vexans males (Table 9). At 1.12 crep, the swarm over the truck increased with approximately 100 individuals involved. A sample of 19 proved to be 58% Ae. vexans males (Table 9). This swarm became steadily smaller until at 1.45 crep, only scattered individuals were present. On 23 July, at approximately 0 crep, a swarm was observed at about 9 m above the ground over a small truck. This swarm was similar in appearance to the one seen on 15 July at 0.14 crep, but fluctuated much more in height from the ground, coming within 4.3-4.6 m from the surface of the road and back up to as high as 15 m. A sample of 17 was taken with a net and all were male chironomids.

Further observations were made on 13 August, an evening with light winds and a clear sky. Some smoke was present in the air from the burning of stubble fields. One swarm began to form over the truck at 0.42 crep. Out of a sample of 20, 78% were Ae. vexans males. Swarming lasted about 15 minutes.

Swarming was again observed on 31 August when at 0.29 crep, a large swarm of several thousand individuals was observed over the truck cab parked at the release site. The majority of this swarm was made up of chironomids, but 3% of a sample of 153 were Ae. vexans males. By 0.82 crep, the swarm was greatly reduced, with less than 50 individuals participating. Out of a sample of 18, 17% were Ae. vexans males.

ii) Sanford site. On 4 September observations were made at the second site, 2.5 km south of the Sanford release site. One swarm at 0.35 crep, was about 2 m tall and formed over the top of a small car parked on the roadway. This consisted of 93% Ae. vexans males (Table 9).

No further marker swarms were observed over the tops of vehicles parked on roadways at either the LaSalle or the Sanford site. In all, 27 samples were taken on 10 evenings. Observations were attempted on other evenings, but either no mosquitoes were present or no males were seen swarming. Evenings on which no swarming was observed were generally those with cool temperatures or high winds.

3) Mating of Ae. vexans in Nature

Copulation of Ae. vexans was observed only twice during this study. The first copulating pair, at the observation site south of the Sanford R.S., was not confirmed as Ae. vexans, but the pair occurred in what later

proved to be an Ae. vexans swarm. A female flew into the marker swarm and was grasped by one of the males. The couple then drifted away from the swarm on the wind and appeared to settle in nearby grass. The second copulating pair was observed on 13 September on a gravel road 2.6 km south of the second observation site and 5 km south of the Sanford R.S. The swarm of about 50 males was noticed shortly after sunset and the single pair observed coupling was hand collected and appeared to be an Ae. vexans male and female.

Chapter V

DISCUSSION

A) Trapping Methods

1) Capturing Adults

Investigations concerning the methods best used to capture adult female mosquitoes have produced interesting results. The comparative trapping study of 1974 clearly indicated that the C-B trap using a 7 watt clear light bulb run on 110 volt A.C. current and the N.J.L.T. were superior to the other types for collecting adult females. At half the sites the C-B 7 watt trap was superior to the N.J.L.T. This was possibly due to the type of habitat in which it was placed. The N.J.L.T., with its higher exposed bulb, is visible from a greater distance, thus attracting adult females from further afield. The Chant-Baldwin traps, with an enclosed, groundward pointing light would not be visible until the mosquito was close at hand. In areas with a dense canopy and limited air movement, the CO₂ attractant would remain in the area for a longer period, resulting in the increased efficiency of the C-B traps in enclosed areas.

The above mentioned relationship between C-B 7 watt traps and the N.J.L.T. was not confirmed during the 1975 trapping season, when the N.J.L.T.'s captured an average of 1058 adult females per trap and the C-B 7 watt traps

captured only 467/trap/night. The difference between the two trapping seasons can be explained by the placement of the traps. During the 1974 season, all traps involved in the comparative trapping study were placed in similar conditions and within 50 m of each other. In 1975, the N.J.L.T.'s were placed on farm lots, often with cattle feed lots close at hand. These feed lots were aggregation points for large numbers of adult females. In contrast the C-B 7 watt traps were placed in farmyards where few cattle were kept.

The C-B β traps used in 1975 had an average capture of 98 adults/trap/night. These results cannot be compared with the results from the C-B 7 watt traps because of the differences in location of the trap types. C-B 7 watt traps were placed in areas with A.C. electrical outlets, largely farmyards or suburban homes, where humans, pets and farm animals were available for blood feeding. The C-B β traps were placed in isolated conditions where the only blood sources available would be non-domestic animals. Baldwin and Chant (1975) tested these traps and found they were as effective as the C-B battery traps.

Sweep-net collections in tall grass, although not as convenient a method of capturing adults as the C-B 7 watt or N.J.L.T., was important in capturing newly-emerged virgin females which were not attracted by CO₂ or light and must be captured by alternative methods. Sweeping is an effective and convenient means of interception trapping.

2) Recovery of marked adults

a) Sweeping. Sweeping in grass and brush near the R.S.'s proved the most effective means of recovering female mosquitoes prior to their insemination and dispersal. At Pinawa 37 of 39 marked recoveries were taken by sweeping at the R.S. and these were used to determine the length of the female refractory period. In the 1974 Sanford release, similar results were obtained, with 127 females being captured by grass sweeping at the R.S. As with unmarked females, there is little chance of capturing marked females in CO₂ and light traps before they begin to bite and/or disperse. Air sweeping methods used during the 1974 comparative trapping study would tend to be most effective in capturing inseminated females and least effective in capturing males and uninseminated females, as much of the attraction of this method is to the CO₂ produced by dry ice and the sweeper. Grass sweeping does not appear to capture females of a particular age or physiological state but captures them as they rest in vegetation. No marked females were captured by sweeping outside the R.S. due to the low numbers of females captured by this method. Trapping methods which recover small numbers of females would not be expected to recapture significant numbers of marked females.

b) Chant-Baldwin traps - battery and beta light.

The C-B battery and C-B β traps were used in the field to

capture marked adult females. The C-B battery traps, used in 1974, captured a total of 8 marked females, 2 at Pinawa and 6 at Sanford (Table 2 and 4). At Pinawa, they captured the only two marked females taken in traps and at Sanford they captured 6 of the 17 marked females taken in traps (Table 2 and 4), indicating the utility of these traps for capturing marked adult mosquitoes.

c) N.J.L.T. and C-B 7 watt. At Pinawa, the 3 N.J.L.T.'s captured no marked adults, possibly due to the small numbers of adults released or due to the open water between the R.S. and the traps. At Sanford, the 9 N.J.L.T.'s captured 11 of 17 marked adults. One trap, located 0.3 km from the R.S. recaptured 9 of the 11 marked adults taken, indicating the usefulness of the N.J.L.T. in this study. Again, in 1975, at the LaSalle release, the majority of marked captures were by N.J.L.T.'s.

The advantage of the N.J.L.T.'s in capturing marked adults at LaSalle, appears to be related directly to the total number of mosquitoes captured. N.J.L.T. #4 at the LaSalle site captured 84% of the total mosquitoes taken in N.J.L.T.'s and captured 70% of the marked adults. Similar results were found for the C-B 7 watt traps, as the trap which captured the largest part of the total C-B 7 watt trap collections (12%) captured 2 of the 3 marked recoveries by C-B traps. These results would indicate that the difference in recaptures between N.J.L.T.'s and C-B

7 watt traps is a function of the total numbers of adults captured.

3) Time requirements of trapping systems

a) Field time. Accurate measurements of the time required to service traps in the field could not be kept, but a general idea of the situation was obtained. New Jersey Light Traps, especially when equipped with timers to turn them on and off at dusk and dawn, required little servicing in the field. The captured insects, dead from exposure to vapona strips, were simply dumped out of their collection jars into a properly labelled cardboard container, and transported to the lab. Occasional trap repairs had to be made and this usually required transport to the lab. Normal servicing involved the replacement of burnt out light bulbs. It was found that a thin layer of plaster of Paris on the bottom of the collecting jars eliminated any moisture problems during trap collections. The N.J.L.T. was also able to operate on weekends as the light and fan operated automatically.

The C-B traps (all types) required more complicated field servicing including battery hook-up on the C-B battery traps and dry ice delivery to all traps. Emptying the traps was a time-consuming operation; involving killing the adults captured, using a pyrethrin or ether spray, and removing the adults from the traps. Servicing of traps at

Sanford took 3 crews of 2 persons from about 09 00 to 12 00 each day. Much of this time was spent in travelling between traps. C-B traps had to be serviced at night again, requiring another visit to each trap, taking 3 people approximately 2 hours each to bait the traps. The nightly baiting required a twice-weekly delivery of dry ice. Because of the time and supply problems, the C-B traps could only be operated 4 nights a week. Moore and Noblet (1974), used a modified dry ice container in a CO₂ trap to capture simulids in Georgia. They were able to store enough dry ice in the container (23 kg) to last 3 or 4 nights of captures. This method, if adapted to the C-B traps used in this dispersal study, would help eliminate a significant portion of the field work.

b) In lab processing. The processing of samples in the laboratory is another important aspect of recapturing efficiency. The processing of materials recovered from traps involved separating adult mosquitoes from other insects and materials taken in the traps, and identification of marked adults. The method of identification of marked adults, once they had been separated from trap collections, did not vary between trap methods and will only be discussed under marking methods. The separation of mosquitoes from the total catch of insects differed greatly between the C-B and N.J.L.T.'s. The N.J.L.T., using a light source and fan, captures a wide variety of

flying insects. Often, the number of non-mosquitoes taken far outnumbers the mosquitoes captured, making it difficult to separate the adult mosquitoes from the others. Mosquitoes are also similar in appearance to other nematoceros diptera which were often taken in large numbers in the N.J.L.T.'s, making identification difficult, especially by a person with little or no experience. Mosquitoes and other small diptera were often entangled in the wings and legs of larger moths and beetles, making it difficult to separate them without damage.

The C-B trap, attracting insects by CO_2 and a small light, selectively captures blood feeding species. Thus the large numbers of other insects attracted to the N.J.L.T. are not attracted to the C-B traps, making the sorting of C-B traps a simple process. Table 8 compares the time 4 students spent sorting N.J.L.T.'s and C-B samples. This table shows the great differences between the two trap types but also demonstrates that there are considerable differences between students.

The type of traps used in a mosquito dispersal study is an important consideration. Although the N.J.L.T. requires more time in the laboratory than the C-B traps, it requires less time in the field. The field time for C-B traps can be reduced by following the suggestions of Moore and Noblet (1974), but this increases the cost of dry ice used to operate the traps.

B) Marking methods

The dispersal studies of 1974 and 1975 utilized two separate marking methods, a dye solution and ^{32}P . Each of these methods were tested for one summer and their suitability for marker and recovery studies noted. Provost (1974) stated that "if work with marked mosquitoes is undertaken in the field, every effort should be made to squeeze the utmost information that can be gotten out of every single marked recapture. It is possible now to establish for recovered females (1) whether or not inseminated (2) degree of parity (3) energy reserve state and (4) occurrence of recent nectar feeding. These parameters can lend much more meaning to the findings of a dispersal and longevity study". The ability to determine these conditions is regulated by the field researcher's ability 1) To mark large numbers of adults 2) To recapture sufficient numbers to obtain a representative sample (a process determined by the trapping methods discussed above) 3) Quickly and without harming the condition of the trap collection, to make the identification of recaptured adults and proceed with tests for insemination, parity etc. The effectiveness of this last procedure is determined by the type of marking method used.

1) Dye marking

The dye marking methods used in 1974 and described in the methods, permitted the researcher to proceed on

several of the points mentioned above. Marking large numbers of newly emerged adults was easily accomplished by quickly removing the pyramid cages from above the pools and placing them on a dry patch of grass for marking. After recapture and identification, marked adults are usually fresh and easily dissected to determine insemination and other conditions. This gives the researcher much access to information from his recovered female mosquitoes.

The dye marking method of identifying marked adults presents one major problem, viz it is very slow. Each captured adult must be separated from trap collections and placed neatly on sheets of towel as described in the methods. This requires an enormous expenditure in time and manpower, especially when N.J.L.T.'s are used to capture marked adults.

When handling dye marked mosquitoes, one is also likely to fall behind in separating and identifying marked adults. This results in drying of specimens, which ruins them for most of the purposes suggested by Provost (1974). This problem can be partly controlled by freezing the trap catches, but even these will dry out with time.

2) Radioactive isotope (^{32}P)

The use of the isotope ^{32}P to mark mosquitoes in their rearing pools has one major advantage over the use of dye markers. Adults, captured in traps, do not have to be separated for identification to take place. The

whole mass of captured insects, excluding large beetles and moths, can be scattered across a pre-packed medical x-ray film and stuck in place with canned glue. In this manner, small samples can be counted to estimate the number of adult mosquitoes in a trap and a trap collection from one night can be exposed to the x-ray film without extensive separation of adults. This results in a great reduction in time and effort. This method does not allow for the identification or dissection of marked recoveries, thus limits its usefulness to dispersal and longevity studies only.

Adults marked with ^{32}P are detectable as long as their radioactivity emission is sufficiently above background to produce spots on x-ray film. At LaSalle ^{32}P marked adults were recorded up to 16 days beyond release. Lab experiments conducted indicated that an exposure 1 day prior to emergence to $.01\mu\text{Ci/l}$ of ^{32}P in their rearing pools produced an average of 581 CPM in a low energy Beta counter after 7 days (range CPM 27-1422). To obtain similar results after 20 days, larvae need to be exposed for 2 days at $.01\mu\text{Ci/l}$. Field results indicated problems with ^{32}P marking. Larvae and pupae collected ranged in their exposure to ^{32}P from 1-4 days. Samples of adults emerging from the pools were poorly marked (Table 5). The low count was due to the short time the larvae from LaSalle were exposed and possibly due to the binding of the ^{32}P to elements in the pools such as detritus and algae. The

low levels of radioactivity in emerging adults made it difficult to identify marked specimens after approximately 1 half life of ^{32}P (14.3 days).

In general, dye marking is effective if the researcher is able to keep up with the daily trap catches. This problem is partly solved by using C-B traps which eliminate much of the lab work load. Radioactive marks appear to be only effective in longevity and dispersal studies. Further work should be done to determine a method which combines the best features of both dye marking (non-destruction of marked adults, ease and reliability of application) and ^{32}P marking (ease of identification). Sinsko (1976) has suggested a florescent dust-gum Arabic marking method which should combine the better qualities of the systems discussed here.

C) Dispersal

These initial studies, conducted at Pinawa and Sanford, indicated that the marking dye and C-B, N.J.L.T. method of mark and recapture were adaptable to conditions in Southern Manitoba. Results similar to those obtained by previous workers were obtained. Chant and Baldwin (1972) using only the C-B traps were able to recover thirty-one ^{32}P marked adults of Ae. communis, 0.12% of the total release. At Pinawa, only 2 marked adults were taken in C-B traps but a total of 37 were recovered by sweeping at the R.S., for a total of 39. The study at

Pinawa was hampered by the small numbers of adults marked.

At Sanford, a combination of N.J.L.T.'s and C-B traps recovered 0.01% of the adults marked (17 of 175,000). Shemanchuk et al. (1955) recovered 0.02% of the radioactively marked Ae. flavescens using sweeping as the recovery method. If sweeping for adults is considered at Sanford, 0.08% of the marked adults were recovered. This does not include 32 marked male Ae. vexans recovered by sweeping (Table 3).

Studies using ^{32}P as a mark proved to be less successful, as only 14 marked adults were taken by traps and 6 by sweeping at the R.S., despite the fact that twice the number of marked adults were released. Some of this difference may be due to the differences in the Sanford and LaSalle areas, Sanford being a more sheltered area with greater protection from the wind. However, the lack of success in 1975 at LaSalle is most likely due to the low level of radioactivity in the adults treated with ^{32}P .

Chant and Baldwin (1972) recovered marked Ae. communis adults up to 44 days and 1.6 km from their R.S. with an indication that dispersal went well beyond the 1.6 km radius of the R.S. My results in 1974 at Pinawa indicated less movement by adult females, which appeared to remain in the immediate vicinity of the R.S. for 7-8 days, the time required for the females to be inseminated. These observations are more in line with the work of

Jenkins and Hassett (1951) and Nielsen (1957) who felt Ae. communis to be a relatively sedentary species.

Data from both LaSalle and Sanford indicated that a significant number of newly emerged adult Ae. vexans did not disperse far from the emergence site, as the majority of recaptured adults were captured in traps within 0.5 km of the R.S. at Sanford and 2.4 km of the R.S. at LaSalle. However, at both Sanford and LaSalle, a few adults were captured at the very perimeter of the trapping area, on the night following release (at 3.9 km in 1974 and 5.2 km in 1975). One adult was captured at 17.7 km, 6 days after release in 1975. This indicates that a part of the emerging population moves quickly out of the area. A second segment of the population remains behind and slowly disperse within the general area of the R.S., possibly not dispersing until after insemination occurs. This was also indicated by the behaviour of the adults when they were released from their pyramid holding cages in 1975. The released adults were free to fly in any manner they chose as no dye had been sprayed onto them. A part of the population, appearing to be about 50%, settled quickly to the grass in the area of the pools, while another segment of the population became very active, flying directly upward through the trees toward the bright sky. This segment may represent a migrating population as described by Provost. Nayar and Saurman (1969) described a migrant

mosquito as being most active on the first night after emergence, the individual showing agitated behaviour in cages and flight behaviour if free.

In 1975 at LaSalle, all marked recoveries were from the R.S. and sites located north of the R.S. This was to be expected, as it has been shown by various workers (Klassen 1968) that adult mosquitoes disperse downwind at times when wind speeds exceed the ideal limits for flight (3-6.5 km/h). During 1975, wind speeds averaged 14.9 km/h from the south (Normal: 16.25 km/h from south at Winnipeg International Airport). This indicates that under normal conditions, mosquitoes dispersing with the wind from the LaSalle area directly south of Winnipeg, will move north toward the city. Other factors, such as the position of the setting sun and the lights of Winnipeg relative to LaSalle would generally produce a northward dispersal of adult mosquitoes. Horsfall (1951) and Gunstream and Chew (1964) indicated that adult Ae. vexans tend to move in the direction of the illuminated sector of the evening sky. During summer evenings at the LaSalle R.S. the northwest and northern sections of the sky were brightly illuminated by the combination of setting sun and the city lights of Winnipeg. The two conditions of wind and light would regularly affect the movement of adult mosquitoes located close to the southern part of Winnipeg.

A northward dispersal was not indicated in the 1974

Sanford release. The Sanford site (Fig. 2) only 12 km east of the LaSalle site, was an area heavily protected by trees around the LaSalle River. These trees would diminish the effects of wind and reduce the effect of lights on the orientation of mosquitoes within the immediate environment. Local winds, farm lights and farm animals would also affect the movement at Sanford more than in the more open area of LaSalle.

D) Insemination of females

Some information of the refractory period in Ae. vexans and Ae. communis is available from this study. At Pinawa, no mated females were recovered until 8 days after the end of the marking period (Table 1). This indicated a refractory period in female Ae. communis similar to that reported by Brust (1971). These data from Pinawa could represent a portion of the population which was subject to an 8 day refractory period during which it did not disperse, rather than the refractory period of the entire population. Chant and Baldwin (1972) believed that newly emerged Ae. communis dispersed rapidly beyond 1.6 km and only returned to the release area later in response to the CO₂ from traps. My results would indicate that in part, Chant and Baldwin's results were due to the refractory period of the females, which would not be attracted to CO₂ traps until after mating.

At Sanford, few unmated females were recovered from

traps. However, in sweep samples in the immediate vicinity of the R.S., mated females did not occur until 8 days after the marking period (Table 3). One female captured on the first day after marking at 3.9 km from the R.S. was mated. This would indicate that one group of females were inseminated early, and rapidly left the area. Being inseminated, these early dispersing females would react to the CO₂ produced by traps. Other females, remaining near the R.S. until mated, did not begin to disperse until later.

E) Swarming

The swarming behaviour of Ae. vexans has not previously been described. In this study, Ae. vexans males were observed swarming in both top swarms and marker swarms. Ae. vexans were observed swarming with at least three other species (Table 9); other unidentified species were also present. Species never sampled in swarms were also present (Table 10).

In top swarms, Ae. vexans and Cx. tarsalis were the least abundant species (Table 9). Cx. restuans and Ae. spencerii were the most abundant species in top swarms (Table 9). The sampling of top swarms in this study was largely incomplete as many top swarms that were observed during the study period went unsampled. Marker swarms were found to contain male Ae. vexans, Ae. spencerii, Cx. tarsalis and Cx. restuans as well as female mosquitoes

and other insects. In marker swarms formed without the presence of an automobile or other object protruding from the roadway, Ae. vexans was found with no other male mosquitoes except those of Cx. restuans, which made up 10% or less of both samples in which they were present.

Marker swarms appearing over an object protruding from a roadway tended to be larger than the other swarms observed, indicating that the presence of the object on the visual contrast marker increased the stimulus to swarm. Other species, not found in marker swarms, but present in top swarms, were present in this variation of the marker swarm, indicating that some other male mosquitoes were also using the object protruding from the roadway as a top swarm marker, at the same time as the marker swarm was occurring.

Marker swarms of Ae. vexans occurred at various times during the evening and appeared to some extent to be regulated by the wind conditions, with winds of 10-15 km/h or more inhibiting the swarming. Further studies may indicate the preferred illumination for starting and ending of swarming behaviour, but this cannot be obtained from the data available at present. It is however, possible to make a general statement, from notes taken in the field, that Ae. vexans appears to begin swarming at a later time than other species, or perhaps begins swarming at a higher altitude (approximately 20 m and up) above a swarm marker and slowly descends in order to keep the swarm marker at a

preferred illumination level. This is supported by unpublished observations, as well as published records (Burgess and Haufe, 1960; MacCreary, 1941; Blakeslee et al. 1959). Although not always sampled, it was generally noted that top swarms began to appear earlier in the evening than Ae. vexans marker swarms. Swarms were also noted above the observer's head at about 20 m above the roadway, out of the reach of a sweep net. One of the swarms was sampled, but it proved to contain no Ae. vexans males. This swarm however, was not behaving in a fashion similar to others seen at this altitude. Other workers (MacCreary, 1941; Blakeslee et al., 1959; Burgess and Haufe, 1960) have observed or collected large numbers of Ae. vexans males at altitudes between 6 and 30 m above the ground. Burgess and Haufe (1960) suggest these may be mating swarms.

Chapter VI

SUMMARY AND CONCLUSIONS

A) Summary

Ae. communis were found to disperse only a few hundred meters from their emergence site. Females were found to have a refractory period of 7-8 days and to remain close to their emergence site until after mating occurred.

Ae. vexans were shown to disperse up to 17.5 km, although most dispersed less than 1.5 km. A refractory period of 7-8 days was noted for non-migrating Ae. vexans. Adults did not disperse until after insemination, except a few captured at 3-17 km immediately after marking.

The C-B 7 watt trap was found to be as effective in capturing adult Aedes mosquitoes as the N.J.L.T. The N.J.L.T. required less field service than the C-B 7 watt traps but N.J.L.T. catches required more time in the laboratory. C-B battery and C-B β traps were useful in capturing adult Aedes in isolated areas not equipped with electrical service.

Ae. vexans were found swarming in single species marker swarms and in mixed marker swarms when these formed over objects protruding from a visual contrast marker. Ae. vexans males were found in top swarms, but only in small numbers.

B) Conclusions

1) Dispersal

The three experiments, conducted at Pinawa, Sanford and LaSalle, demonstrated the usefulness of the plastic lined pools and the pyramidal cages in conducting mark and recovery studies on mosquitoes. The transport of larvae and pupae in sealed buckets in a vehicle permitted one to travel long distances to collect the juvenile stages and transfer them to a distant release site. This extended the usefulness of the mark-recovery method.

These studies have shown that the two marking methods used, dye and ^{32}P , although useful in mark and recovery studies, are far from ideal. Of the two, marking with dye is preferred as it facilitates the gathering of data on each marked recovery. New methods as suggested by Sinsko (1976) may eliminate many of the problems experienced in the present study.

Little difference was noted in the effectiveness of N.J.L.T.'s and C-B 7 watt traps in capturing adult mosquitoes. Differences between the two trap types were related to processing time in the field and the laboratory. The C-B β traps, although not as effective as the C-B 7 watt traps, are useful in isolated areas. It is recommended that future dispersal studies use the N.J.L.T. as this trap takes a less selective sample of the mosquito population in

an area and captures far greater numbers of mosquitoes nightly. However, C-B~~B~~ traps should prove effective in areas where no electricity is available.

Sweeping for marked adults at the R.S. was the most effective means of recapturing virgin females and males. This method should be continued following all future releases in order to obtain information on insemination and dispersal.

The dispersal of Ae. communis at Pinawa was not studied sufficiently to show any definite pattern. The study suggested however, that Ae. communis does not disperse widely but remains close to its emergence site, especially until insemination occurs. This is in contradiction to the findings of Chant and Baldwin (1972) but agrees with Jenkins and Hassett (1951).

The two dispersal tests conducted on Ae. vexans did not produce enough data to draw conclusions on the dispersal pattern. It appeared however, that there were two distinct populations within the emerging adults; a stationary population which remained near the R.S. until insemination occurred and then began to disperse in response to certain stimuli; a second population, represented in the studies by a few catches made shortly after marking, moved quickly out of the area of emergence in what appeared to be a non-appetential flight. Information from LaSalle indicates that a northward dispersal of Ae. vexans, toward

the city of Winnipeg, can be expected. This appears to be in response to the stimuli of an illuminated horizon and a flight direction with the prevailing winds.

Data collected at Pinawa suggests a 7 day refractory period for virgin Ae. communis females. This refractory period appears to affect the dispersal pattern of Ae. communis by keeping the population sedentary until mating occurs. Ae. communis was shown to have a refractory period of 7-8 days in the laboratory by Brust (1971). The refractory period in Ae. vexans also inhibited dispersal of the non-migratory segment of the population.

2) Swarming

The swarming behaviour of Ae. vexans is described as occurring in marker swarms formed over roadways and other ground level visual contrast markers. The presence of a large object protruding from the visual contrast marker intensifies the swarming behaviour, but also attracts males of other species. Marker swarms, except as noted, were almost exclusively Ae. vexans, thus affording a degree of species isolation. Ae. vexans did occur in top swarms, but was almost always mixed with other species. Top swarms generally had small numbers of Ae. vexans.

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