THE UNIVERSITY OF MANITOBA

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

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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 appetence 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 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 Kliewer 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, Kliewer 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. Kliewer 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 terrens, (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 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 CO_2 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), Kliewer and Miura

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. punctor. 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. punctor, 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