

DISPERSAL OF MOSQUITOES

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This review of the literature shows that mosquitoes may undergo displacement of many miles from the site of eclosion. The dispersal of mosquitoes may be influenced by wind, topographical features, vegetation, and by an illuminated sector of sky. Wind, more than any other environmental factor, influences dispersal. The optomotor responses of mosquitoes flying in a wind are useful in predicting the pattern of dispersal.

Vigorous dispersal is vital to the survival of mosquito species. Although it is frequently wasteful (mosquitoes may perish that venture into deserts, over oceans, or to other inhospitable regions), dispersal prevents extinction of the species because of a fluctuating climate, a fluctuating sparsity or distribution of host species, or the vagaries of human activity. Populations may be totally destroyed in parts of the range, but as soon as these areas again become tolerable, the vigorously dispersing emigrants repopulate them, and the reclaimed area may serve as a refuge when other parts of the range become intolerable. Also, vigorous dispersal causes such rapid gene flow between local populations that the genotypes may be repatterned rapidly to meet the new conditions, i. e., changing climate, vegetation, human settlements, or insecticides.

Some *Aedes* species can fly as far as 30 air miles or remain airborne about 12 hours without feeding (Hocking 1953), and *Culex pipiens berbericus* Roubaud can fly no less than 5 km by using reserves carried over from the pupal stage (Clements 1963). However, the extent to which mosquitoes in nature make use of this ability to travel depends on the species, the vicissitudes of weather, the terrain, and on yet unknown factors.

The tendency to disperse varies greatly between species. Some show a marked tendency to disperse great distances shortly after eclosion and before seeking the first blood meal. The best examples are *Aedes sollicitans* (Walker) (Felt 1904), *Aedes taeniorhynchus* (Wied.) (Provost 1957), *Anopheles sundaicus* (Rodenhaldt), *Anopheles saccharovi* (Favr.), and *Anopheles maculipennis* Meigen (see Eyles 1944), and perhaps *Anopheles pharoensis* Theobald (Kirkpatrick 1925) which regularly disperse in large numbers in excess of 10 miles and sometimes in excess of 100 miles from the site of eclosion. Yet, another species such as *Culex tarsalis* Coquillett show

no marked migratory phase between eclosion and the search for the first blood meal; yet this species may spread 25 miles per generation (Bailey *et al.* 1965), and it and others such as *Anopheles quadrimaculatus* Say (Gartrell and Orgain 1946), *Anopheles freeborni* Aitken (Rosentiel 1948) and *Anopheles maculipennis* (see Eyles 1944) may show a prehibernation migratory phase that takes a portion of the population miles from the site of eclosion. Still other mosquitoes such as the domesticated populations of *Aedes aegypti* (L.) (Morland and Hays 1958), *Anopheles culicifacies* Giles (Russell *et al.* 1944) and *Culex pipiens fatigans* (Lindquist *et al.* 1965) do not fly far from the site of eclosion; nevertheless, the first flight of some individuals of *C. pipiens fatigans* is believed to be truly migrational. Almost nothing is known of dispersal of adults that have overwintered.

Populations appear to be heterogeneous with regard to the drive to disperse. Even in the highly migratory *Aedes taeniorhynchus*, a significant number do not disperse beyond a few hundred meters of the site of eclosion (Bidleymayer and Schoof 1957). Perhaps these stragglers emerge too late to profit from the stimuli of twilight (see Provost 1957, Pausch and Provost 1965). However, the tendency to disperse also depends on the genotype of the individual: the motility of one laboratory strain of *Anopheles quadrimaculatus* was found to have been selected away through prolonged colonization (Dame *et al.* 1964). Nevertheless, we lack evidence that selection by insecticides has affected the drive to disperse (Sautet 1957), and Wada (1965) believed that crowding during the larval stadia may increase the drive.

With anophelines, males do not always disperse as widely as females (Eyles 1944), and similar observations have been made for *Aedes taeniorhynchus* (Provost 1957) in which mating may occur before the migratory flight (Haeger 1960). However, Klassen and Hocking (1964) did not find any apparent difference between the sexes of *Aedes cataphylla* Dyar; they mated after the initial long-distance flight. Clarke (1943) calculated the average flights of male and female *Culex pipiens fatigans* and *Aedes vexans* (Meigen) to be 9.8, 10.3, 9.4, and 9.1 miles, respectively.

Behavior and Dispersal

Ross (1905) distinguished between two types of flight: relatively long flights from one "breeding ground" to another and "flitters" or trivial flights near the habitat. The long flight is believed to be an example of nonappetential flight (Provost 1952) (nonpurposive spontaneous flight; Nielsen 1958). It starts shortly after sundown in *Aedes vexans* (Clarke 1943), *Aedes taeniorhynchus* (Provost 1957; Bidleymayer and Schoof 1957; Nielsen 1958), *Aedes cataphylla* (Klassen and Hocking 1964), and *Culex tarsalis* (Bailey *et al.* 1965). The drive to disperse is so pronounced in newly emerged *Aedes fitchii* (Felt and Young) mosquitoes that they will take flight in a wind of 12-14 mph that inhibits the flight of mosquitoes several days old (Klassen and Hocking 1964). In *Aedes taeniorhynchus*, the nonappetential drive to disperse does not persist past the first day of adult life (Provost 1957), but host-seeking females and females searching for resting and oviposition sites do make short appetential (purposive) flights that, though they are markedly influenced by host density, microclimate, and terrain, may add substantially to the ultimate dispersal of

a species (Provost 1957).

Wind and Dispersal

Wind has been shown to be of overriding importance in determining the pattern of dispersal by releases and recaptures of marked mosquitoes and by direct observations of migratory flights (table 1, p. 49). Valuable insights into dispersal may be obtained by a thorough study of the manner in which a mosquito navigates in a wind.

Kennedy (1940, 1951) showed that insects flying in a wind navigate by making compensatory responses to visual stimuli from the relative movement of the ground below them. His optomotor hypothesis of navigation postulates that an insect flying in certain windspeeds and at certain heights above the ground will orient into the wind; at other heights and windspeeds, it will orient downwind. Observations in the field by Steiner (1953), Haeger (1960), Klassen and Hocking (1964), and Bailey *et al.* (1965) support Kennedy's hypothesis.

The manner in which a flying insect controls its track is somewhat similar to the manner in which one controls the path of an automobile. On a straight road with ideal conditions, one prefers to drive so the images pass across the visual field from front to back at, say, 60 mph. If the automobile skids, the movement of the images across the visual field has a transverse component, and the driver immediately reduces this component to zero by reorienting the automobile. On a slippery hill, the automobile may cease to make headway and may slide backwards, a movement detected by the back to front movement of the images; it is prevented either by accelerating or by braking.

The dispersing mosquito has similar reactions; however, its navigation is more complex and can be described mathematically (Klassen and Hocking 1964).

Since the velocity of the images varies as

$$V = w(Z - \lambda) \quad (1)$$

and the windspeed increases as

$$W = \frac{u}{K} \log \frac{Z}{Z_0} \quad (2)$$

upwind flight is described as

$$W(Z - \lambda) = V - \frac{u}{K} \log \frac{Z}{Z_0} \quad (3)$$

and downwind flight as

$$V + \frac{u}{K} \log \frac{Z}{Z_0} = w(Z - \lambda) \quad (4)$$

when z is the height of the mosquito above ground

λ is the height of the vegetation providing the visual pattern

Z is the height of the mosquito above the visual pattern

V is the airspeed of the mosquito

w is the preferred angular rate of apparent movement of the ground from front to back

W is the windspeed at height Z above the ground

u is the friction or the velocity

K is Karman's constant

Z_0 is the roughness length.

Thus the velocity of the images varies inversely with increasing height above the background (1) and because windspeed increases logarithmically with the height above the ground (2). In addition, the mosquito prefers a certain airspeed (cruising speed) (Hocking 1953). Thus, the dispersing mosquito compensates for undesirable visual effects by changing its airspeed within certain limits, by constantly correcting its orientation along the direction of the wind so no side slippage occurs, by turning from upwind to downwind or vice-versa, or by settling.

In a gentle wind, the mosquito takes off against the wind, climbs to an altitude at which the images pass by at a preferred rate, and flies near its preferred airspeed. Upwind flight is described by equation 3. If the windspeed at the altitude of flight exceeds the preferred airspeed, the insect can lower its altitude or even settle. Also, the mosquito may turn downwind (fig. 1a). Then the windspeed added to the airspeed will greatly increase movement relative to the background, and the mosquito must gain altitude so the movement of images will be at the preferred rate. Downwind flight is described by equation 4. Figure 1b shows the permissible heights of flight of *Aedes punctor* (Kirby) in relation to windspeed measured at 500 cm above ground. The lines in this figure were calculated from equations 3 and 4 and represent the values at which stimuli calling for change start to be received. Actually, because these stimuli must reach a minimum threshold, the permissible heights of flight are zones whose width is small when the background is well-perceived and when the altitude is low. Figure 1c shows the relationship between windspeed and maximum rate of displacements of *Aedes punctor* and *Aedes aegypti* in upwind and downwind flight. Theoretically, the weak flier, *Aedes aegypti*, should be able to disperse upwind and downwind at the same rate when the windspeed at 500 cm above ground is about 120 cm/sec (2.6 mph). At greater windspeeds, downwind displacement increasingly predominates. Also, theoretically, the moderately strong flier, *Aedes punctor*, should be able to disperse upwind and downwind at the same rate when the windspeed at 500 cm is 160 cm/sec (3.5 mph). However, experience (table 1) indicates that in these cases, downwind dispersal would predominate, probably because at the start of migratory flight, mosquitoes climb to fairly high altitudes at which, according to equation 4, only downwind flight is possible.

Clarke (1943) observed with regard to *Aedes vexans* that "during the period of emergence ... *vexans* rises from the marsh singly and continuously at dusk for a period of approximately one hour. They are observed to rise to a height of 40 feet and fly with the wind." Similarly, *Aedes taeniorhynchus* climbs at an angle of 30-60° to above the mangroves (Nielsen 1958, Haeger 1960, Provost 1957). Also, Bailey *et al.* (1965) observed that "when swarms of *Culex tarsalis* emerged from the rice fields in the early evening they would spiral upward in an irregular manner to heights of 12 to 15 feet, according to the temperatures of the atmospheric layers, and then would level off in the wind current." These authors found that *C. tarsalis* usually flies at altitudes between 1.5 and 15 meters (5 and 50 feet). *Aedes cataphylla* rises to 4 to 8 meters, depending on the speed of the wind (Klassen and Hocking 1964). Somewhat similar behavior was observed for *Culex pipiens fatigans* (Lindquist *et al.* 1965) and for *Anopheles gambiae* Giles (DeMeillon 1937).

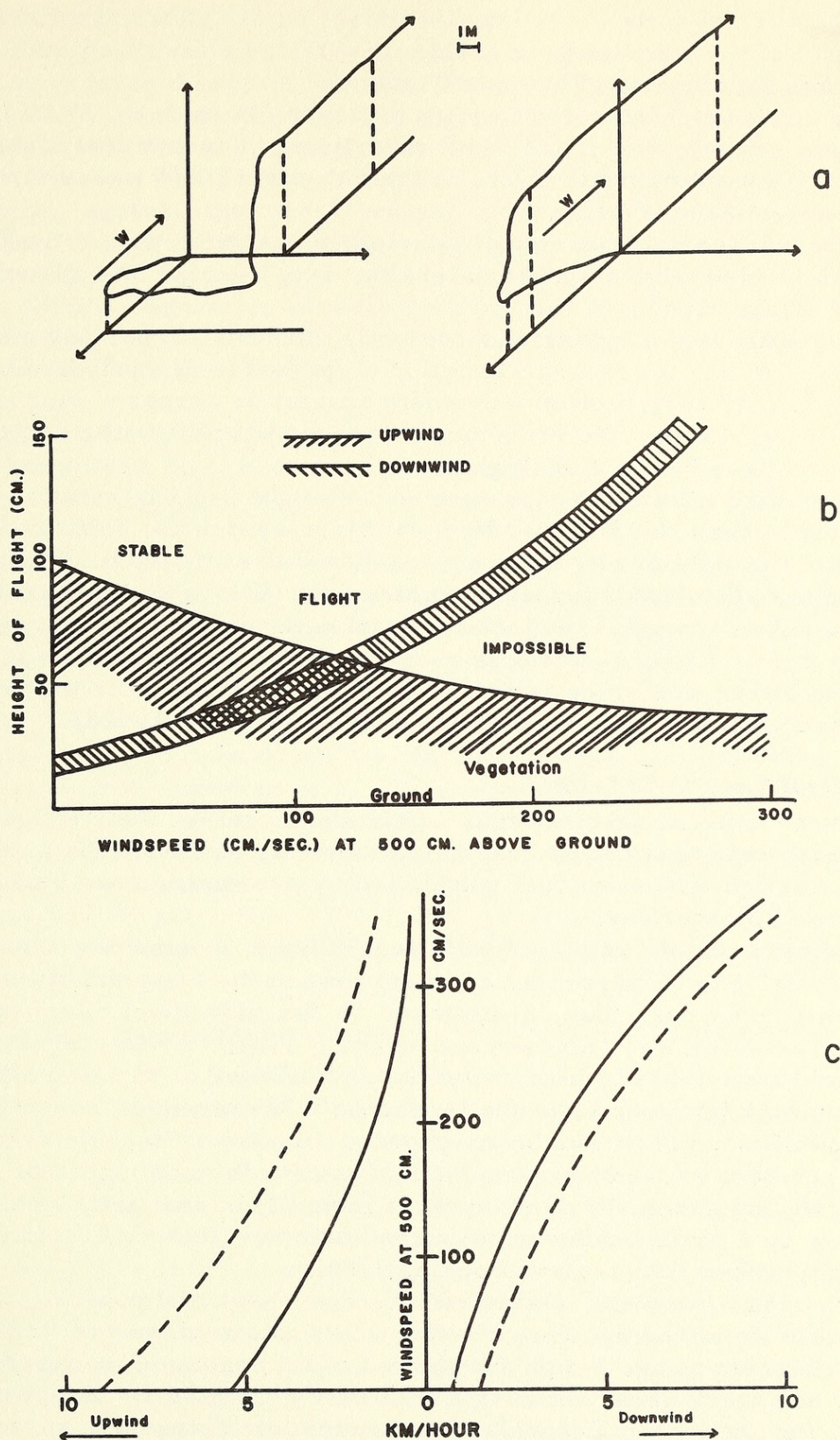


Fig. 1 a, Paths of *Aedes cataphylla* take-off into a wind W , on a plain. b, The permissible heights of flight of *Aedes punctor* in relation to windspeed at 5 m above ground. c, The relationship between windspeed and the max. displacement rate of *A. punctor* (---) and *Aedes aegypti* (—) in upwind and downwind flight. Redrawn from Klassen & Hocking (1964) with permission.

The observations of Bailey *et al.* (1965) on the effect of wind on the dispersal of *Culex tarsalis* agree precisely with the effect predicted by the optomotor hypothesis. They found that:

- "1. At low wind velocities, up to 2 mph (94 cm/sec, W.K.), dispersal takes place in all directions. The greatest distance of recapture was 2.75 ... against a wind of 0 to 2.9 mph (136 cm/sec, W.K.).
2. At least 10 per cent of the mosquitoes from any particular release may disperse laterally, i.e., across the direction of the wind.
3. Above a limiting wind velocity of about 4 mph (188 cm/sec, W.K.) the general direction dispersal is downwind. There is only very limited movement against or across a wind as high as 4 mph. No recaptures were made upwind when velocities were 5.4 mph or higher ...".

Moonlight allows the phenomenon of twilight flight to continue (Rees 1945, Ribbands 1945, Provost 1958, Bidlingmayer 1964) because the intensity of the light at full moon approaches that at twilight. The eyes of mosquitoes are adapted for vision in dim light (Sato *et al.* 1957), and their wide visual solid angle is especially suitable for maintaining a track even in dim light. Also, mosquitoes respond to the plane of polarized light (Kalmus 1958), and since polarization of skylight is maximum one hour after sundown, mosquitoes may use it as a navigational aid.

Dispersal and Topographical Features

Topographical features may affect dispersal by their influence on micrometeorological conditions, i.e., they may influence the prevailing wind and the creation of local winds, and by presenting visual stimuli to dispersing mosquitoes.

Evidence exists that, in the absence of wind, mosquitoes with a pronounced drive to disperse tend to orient toward the low point of the horizon; this response, then, contributes to the movement of mosquitoes into and along valleys (Klassen and Hocking 1964). Are dispersing mosquitoes attracted to prominent sections (skototaxis) or are they attracted to low points (hypsoaxis) of the landscape? Movement of mosquitoes up the side of mountains has been recorded (Hearle 1926); however, this may have been caused by upwind orientation to the sloping wind.

Also, the assembly of mosquitoes in wooded areas may be directed not only by a taxis but by wind-borne moisture that causes an upwind orientation (see Klassen and Hocking 1964).

On clear evenings, plains radiate their heat and cool the air immediately above them. This cool air sinks into ravines and flows down river channels at ca. 5 mph (measured at Edmonton, Canada; Klassen 1962), and these local winds are not usually affected by the prevailing wind. Perhaps river channels thus accumulate dispersing mosquitoes and then channel their movements up or down a valley (Klassen and Hocking 1964). During dry seasons in the Transvaal, dispersal is restricted to wooded river valleys (DeMeillon 1933 as cited by Horsfall 1965). Similarly, dispersal of *Aedes vexans* and *Aedes aldrichi* occurred mainly along the Columbia River Valley and its tributaries and not on the plain (Stage *et al.* 1937). Causey and Kumm (1948) recaptured most

tagged mosquitoes within a river valley.

In deep valleys (fig. 2), winds blow up their sides and up-valley by day and reverse direction by night (Defant 1951). By flying against the down-valley wind during a single night, female *Anopheles maculipennis* may disperse into human settlements no less than 5 km from the site of eclosion (Ivanova 1962). Moreover, female mosquitoes locate their hosts by flying against the scent-bearing downslope wind (Ivanova 1962).

Near bodies of water, a wind may blow from water to land by day and reverse at night. These winds, too, affect dispersal patterns (Ivanova 1962). Regularly, an early evening wind from the Pacific is channelled along the Sacramento River and affects the up-valley dispersal of *Culex tarsalis* (Bailey *et al.* 1965).

Movement along Lines or Borders

Mosquitoes have been observed to orient and move along lines or borders, irrespective of the wind (Jenkins and Hassett 1954, Snow and Pickard 1957). Recently, Giglioli (1965) observed that *Anopheles melas* (Theobald) traveled 1 to 2 miles from the site of eclosion to a village by following the interface between bushes and cleared land. The mosquitoes formed streams about 20 to 60 feet wide, flew below an altitude of 5 feet, and did not align with the direction of the wind.

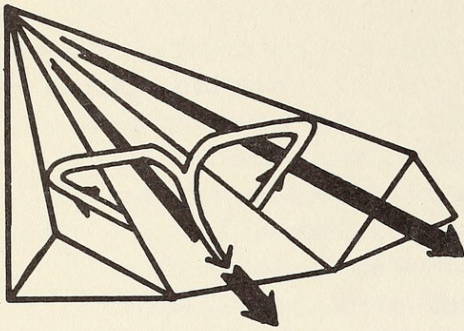
Movement with Strata of Vegetation

Horsfall (1955) reported that the movements of mosquitoes may be restricted to the undergrowth. "Females were moving eastward in the undergrowth of a forest area during a sultry afternoon when no wind was blowing. The females flitted from one low plant to another, but always in the same general easterly direction." Such creeping migration seems to occur in Utah also; Rees (1945), too, noted that females followed paths above a low canopy of vegetation and that a flight moved 8 km in 2 to 5 days in this case.

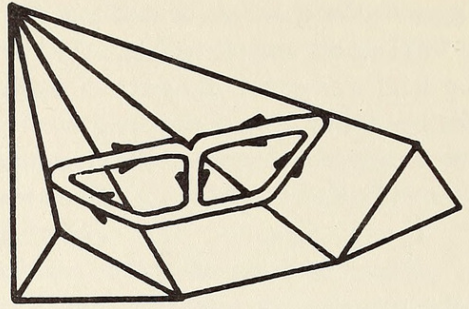
Movement toward Illuminated Sector of the Sky

Horsfall (1955) reported that a mass flight of *Aedes vexans* took place toward "the flowing skyline caused by suburban glowing lights." Similarly, Gunstream and Chew (1964) observed that this species may orient to the strongly illuminated western sky rather than to the wind. Orientation of Coleoptera to a lighted section of the horizon has been demonstrated by Lindroth (1948) and deserves investigation.

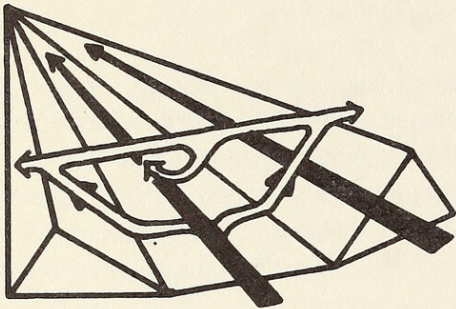
MacCreary (1939) operated 5 light traps in Newark, Delaware, and found that the catch in each varied. He felt that the mosquitoes were observed to fly toward areas that had the highest population density of man and cited the opinion of Headlee (1936) that "Both *Aedes vexans* (Meig.) and *Culex pipiens* L. tend to migrate in the direction of great populations regardless of the wind direction." Similarly, Gillies (1961) found the dispersion of *Anopheles gambiae* was related primarily to the distribution of human settlements. Perhaps the lights of human settlements are attractive, or perhaps the mosquitoes simply accumulate near the blood source by klinokinesis. Ivanova (1962) believed that mosquitoes several kilometers distant from a human settlement responded to human odors carried on katabatic winds.



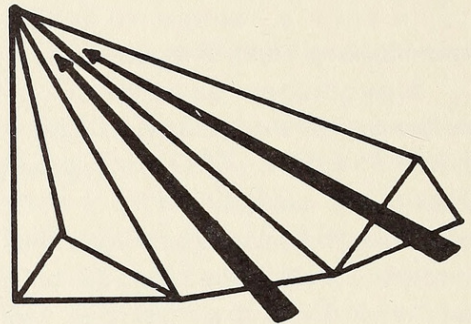
SUNRISE



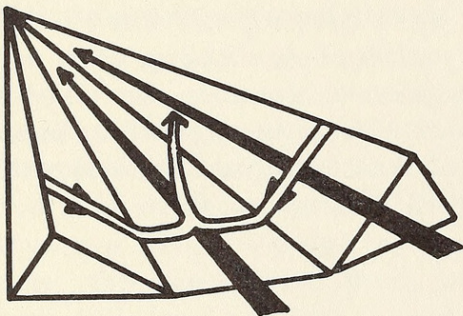
FORENOON



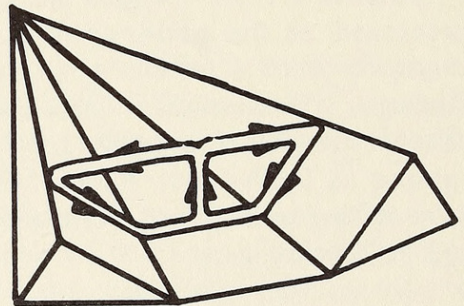
NOON



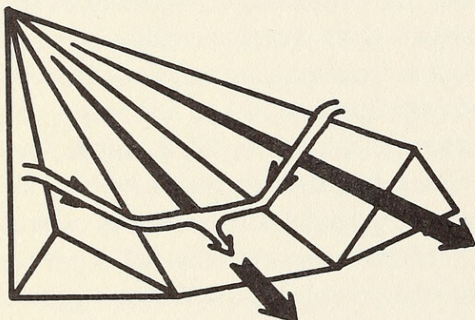
AFTERNOON



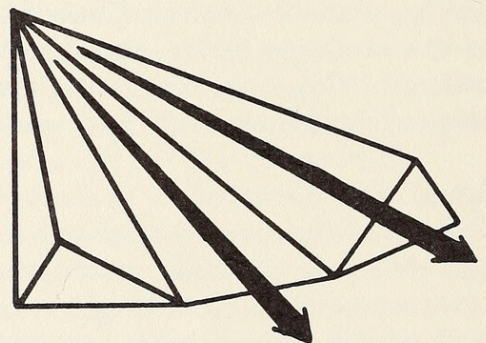
EVENING



EARLY NIGHT



MIDNIGHT



BEFORE SUNRISE

Fig. 2. Air currents within a large valley at various times of day. Based on Defant's (1951) model of the valley-slope wind system.

Passive Transport of Mosquitoes

Movements of mosquitoes other than those near the surface of the earth have been reported. Smith *et al.* (1956) demonstrated with marked mosquitoes that when a cool air mass moved across a semitropical area in California, vast numbers of mosquitoes were picked up and deposited 30 to 60 miles distant from the site of eclosion. Smith (personal communication) explained this transport as follows: "I do not have any air temperature data of the moving air but would assume it would not be much below 10° lower than the valley air ... I do not believe this mass could be considered as passing over in the nature of a frontal movement. Meteorological information indicated that it was a local movement drawn in from the coast over about 60 miles of low hot hills to fill a local barometric low and dissipated once it entered the valley. My belief is that the mosquitoes were not carried on this cool air or any local surface movement it set up, but were stimulated by cool air and carried by thermal currents at higher altitudes ...".

A mass transport of *Aedes vexans* in a cold front was described by Horsfall (1954). Perhaps storm cells of the advancing air mass picked up the mosquitoes and carried them high into the air as is apparently also the case with the spruce budworm moth, *Choristoneura fumiferans* (Clemens) (Greenbank 1956). Some species of mosquitoes were caught by Glick (1939) at 3000 feet and 5000 feet over the central United States, and adult *Culex tarsalis* were taken at 500, 1000, and 2000 feet over Texas (Glick and Noble 1961). Also, Bailey *et al.* (1965) trapped this species at the top of a 1540-foot television tower in California.

Changes in pressure associated with the passage of cold fronts "excite" some Diptera (Wellington 1945, 1946), and Haufe (1954, 1963) demonstrated that *Aedes aegypti* exhibits increased activity with such changes. Moreover, Kennedy (1940) and Kalmus and Hocking (1960) showed that mosquitoes take flight when windspeeds are decreasing. Conceivably, mosquitoes, particularly newly-emerged ones, could be picked up by frontal systems as a result of their flight activity.

Armstrong (1963) felt that observations are needed to determine whether the low-level jet streams that develop above temperature inversions on the Great Plains could transport mosquitoes. The chances seem small that significant numbers of mosquitoes would be entrained into these jets that occur at a height greater than 800 feet above the plain.

Also, mechanical dispersal of eggs or larvae of *Aedes aegypti* in water containers moved along commercial routes has expanded the range of this species (MacDonald 1956).

TABLE 1. Reports on the influence of wind on mosquito dispersal.

Species	Maximum distance flown (miles)		Remarks	Sources
	Upwind	Downwind		
<i>Anopheles:</i>				
<i>albimanus</i> Wiedemann	1		4 mph wind.	LePrince (1912)
<i>funestus</i> Giles	< 0.75	2.8		DeMeillon (1937)
<i>funestus</i>	< 4.5	3.25	Other specimens seen fly- ing with wind.	Adams (1940)
<i>gambiae</i>	< 4.5	3.25	Other specimens seen fly- ing with wind.	Adams (1940)
<i>gambiae</i>		< 2		DeMeillon (1937)
<i>maculipennis</i>		3		Wenyon (1912)
<i>labranchiae</i> <i>atroparvus</i> Van Thiel		< 8.7	Many more downwind than upwind.	Swellengrebel (1929)
<i>minimus</i> <i>flavirostris</i> (Ludlow)	< 0.25	< 1.4	Strong wind.	Russell & Santiago (1934)
<i>pharoensis</i>		5.6		Low (1925)
<i>pseudopunctipennis</i> Theobald	< 3.7	< 3.7	Most flew upwind.	Rickard (1928)
<i>sundaicus</i>			Flew 4 miles, windspeed negligible.	Van Breeman (1920)
<i>culicifacies</i>			251 downwind, 69 upwind, 145 crosswind, max. < 1.75.	Russell <i>et al.</i> (1944)
<i>pharonensis</i>		< 18-28	Downwind migrations over desert at full moon	Garrett-Jones (1950)
		45	"looked like a dust storm."	Kirkpatrick (1925)
<i>minimus</i> <i>flavirostris</i>			Rough terrain, windspeed and direction variable, max. distance 1.25 miles, flew in all directions.	Ejercito & Urbino (1951)
<i>vagus</i> var. <i>limosus</i> <i>sollicitans</i>		40	Experiments of Smith. Flew up to 4 miles, per- haps upwind.	Felt (1904) Elmore & Schoof (1963)

TABLE 1. (cont.)

Species	Maximum distance flown (miles)		Remarks	Sources
	Upwind	Downwind		
<i>Anopheles:</i>				
<i>sollicitans</i>		ca. 10	Regularly flies across Delaware Bay.	MacCreary & Stearns (1937)
<i>cantator</i> (Coquillett)		40 ca. 10	Experiments of Smith Regularly flies across Delaware Bay.	Felt (1904) MacCreary & Stearns (1937)
<i>aldrichi</i> (Dyar & Knab) = <i>sticticus</i> (Meigen)		several	Flew along Fraser River valley. Flew up and down Columbia River valley & tributaries.	Hearle (1926) Stage <i>et al.</i> (1937)
<i>vexans</i>		several several	Flew along Fraser River valley Flight mostly restricted to Columbia River valley & tributaries.	Rempel (1953) Hearle (1926) Stage <i>et al.</i> (1937)
		14	Flight of newly emerged adults has strong downwind tendency, windspeed < 34 mph.	Clarke (1943)
		90-230	Cold front following hot weather.	Horsfall (1954)
<i>Aedes:</i>				
<i>dorsalis</i> (Meigen)	5-8		Slow movement, level plain.	Rees (1935)
<i>albopictus</i> (Skuse)	0.11			Bonnet & Worcester (1946)
<i>leucocelaenus</i> Dyar & Shannon			Flight has downwind bias.	Causey & Kumm (1948)
<i>communis</i> (DeGeer)			Flew in all directions < 5000 ft, wind variable in speed and direction.	Jenkins & Hassett (1951)
<i>taeniorhynchus</i>		< 20	Downwind bias, terrain may affect orientation.	Provost (1952)
		25	All downwind 4 days after eclosion.	Provost (1957)

TABLE 1. (cont.)

Species	Maximum distance flown (miles)		Remarks	Sources
	Upwind	Downwind		
<i>Aedes:</i>				
<i>taeniorhynchus</i>	30-60 20		Carried on W or SW wind. Most flew upwind; winds 6-9 mph. Wind somewhat variable, flew up to 18 miles.	Harden & Chubb (1961) Bidlingmayer & Schoof (1957) Elmore & Schoof (1963)
<i>spencerii</i> (Theobald)	several			Rempel (1953)
"blacklegged <i>Aedes</i> "	several			Rempel (1953)
<i>flavescens</i> (Muller)	6.6		Majority moved with prevailing wind.	Shemanchuk (1955)
<i>nigromaculis</i> (Ludlow)	30-60		Probably caught up in convection of cool air mass.	Smith <i>et al.</i> (1956)
<i>aegypti</i>	1.6		In absence of wind dis- persal is "homogeneous"	Wolfensohn & Galun (1953)
	1165		Wind more instrumental in dispersal than flight.	Bugher & Taylor (1949)
<i>cantator</i>	ca. 10		Regularly flies across Delaware Bay.	MacCreary & Stearns (1937)
<i>Culex:</i>				
spp.	< 18-28		Migrations over desert at full moon.	Garrett-Jones (1950)
<i>tarsalis</i>	2.5	1	Variable wind.	Reeves <i>et al.</i> (1948)
		15.75	3-4 mph wind carries mosquitoes 5 miles down- wind in 1 night. Some fly upwind. At low windspeeds, mosquitoes fly in all directions.	Bailey <i>et al.</i> (1965)
<i>quinquefasciatus</i>			Shifting wind; flew in all directions and up to 3.5 miles.	Fussell (1964)
	1			Reeves <i>et al.</i> (1948)
<i>Culex:</i>				
<i>pipiens fatigans</i>			Flew 900 yds, "with a strong wind, dispersal would be increased".	Burton (1965)
		14		Clarke (1943)
<i>salinarius</i> Coquillett	ca. 10		Regularly flies across Delaware Bay	MacCreary & Stearns (1937)

TABLE 1. (cont.)

Species	Maximum distance flown (miles)	Remarks	Sources
	Upwind	Downwind	
Other genera:			
Unknown	22	Several genera; "slow steady breezes brought large numbers over desert".	Davis (1901) Causey & Kumm (1948)
<i>Stegoconops spegazzinii</i> (Brethes)		Flight has downwind bias	Quarterman <i>et al.</i> (1955)
<i>Psorophora</i> sp.	< 6	Strong tendency to move downwind.	

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