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Trajectory analysis of winds and eastern equine encephalitis in USA, 1980–5

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SUMMARY

Backward trajectories of winds were determined to identify possible sources of eastern equine encephalitis virus associated with isolation of virus from mosquitoes or birds or outbreaks in horses between 1980 and 1985 in Maryland, New Jersey, New York and Michigan, USA.

The results of the trajectory analyses suggested that eastern equine encephalitis virus could have been carried by infected mosquitoes on surface winds at temperatures 13 °C or higher from North Carolina north-eastwards along the Atlantic Coast to Maryland and New Jersey and thence to upstate New York and from western Kentucky to Michigan. Landing of mosquitoes was associated with the presence of a cold front and rain leading to variations in the location and timing of outbreaks from year to year. The mosquito responsible was most likely to have been *Culiseta melanura*, but *Coquillettidia perturbans* and *Aedes sollicitans* could also have been involved.

There may be a continual cycle of eastern equine encephalitis virus in mosquitoes and birds in south-eastern USA, from where the virus could be distributed by infected mosquitoes on the wind along the Gulf and Atlantic Coasts and up the Mississippi Valley.

INTRODUCTION

In a previous paper [1] we found by trajectory analysis of winds that in northern USA and Canada the timing and location of outbreaks of western equine encephalitis (WEE) in horses and man as well as seroconversion in chickens, the increase in *Culex tarsalis* numbers and the isolation of WEE virus could be correlated with warm southerly winds meeting cold fronts associated with rain. It was suggested that WEE virus was introduced to these northern areas by *Cx. tarsalis* mosquitoes infected with WEE virus carried on southerly winds.

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Eastern equine encephalitis (EEE) causes disease in horses, man and pheasants in the eastern United States along the Atlantic seaboard, on the Gulf Coast and northwards to Michigan. The causal virus is transmitted by mosquitoes. The method of overwintering is not known. Local survival of virus in adult mosquitoes, mosquito larvae or eggs or in resident birds has been suggested; or there may be annual re-introduction by migratory birds or mosquitoes [2]. Sellers [3] analysed outbreaks of EEE in 1972 in Connecticut, USA and Quebec, Canada. Examination of surface and 850 mb weather maps for the periods before the first outbreaks indicated that the outbreak in Connecticut could have originated from infected mosquitoes carried on the wind from New Jersey or even as far south as Georgia, and that infected mosquitoes could have been carried north from Connecticut to start the outbreak in Quebec. However, weather data for 1972 were not available in the data bank of the computer model to analyse backward trajectories of winds. It was therefore decided to examine backward trajectories of winds for outbreaks of EEE in horses and isolations of EEE virus from mosquitoes and birds in the USA for years between 1980 and 1985.

BACKGROUND DATA

Virus, hosts and vectors

Two antigenic variants of EEE virus, North American and South American, have been distinguished by the short-incubation haemagglutination inhibition test [4].

The hosts are birds, horses and man. In birds viraemia lasts from 1 to 5 days after infection, with titres high enough to infect mosquitoes. Pheasants may die as a result of infection [2]. In horses encephalitis is seen 4–10 days after infection; fever occurs on the second day [5]. Viraemia lasts for 1–5 days and occasionally reaches a titre capable of infecting mosquitoes. Man is regarded as a dead-end host.

The main species of mosquito implicated in transmission include *Culiseta melanura*, *Aedes canadensis*, *Ae. sollicitans*, *Ae. vexans* and *Coquillettidia perturbans* [6]. *Cx. salinarius*, *Ae. cantator*, *Psorophora confinnis* and *Ae. taeniorhynchus* may also be involved, especially in southern USA [2, 7]. *Cs. melanura* and *Cq. perturbans* overwinter as larvae, the *Aedes* species as eggs. *Cs. melanura* feeds mainly on passerine birds, but later in the season may feed on mammals including horses and man [8, 9]. *Aedes* species, *Cq. perturbans*, *Ps. confinnis* and *Cx. salinarius* are mainly mammal biters but also bite birds [10].

At low wind speeds and within their boundary layer mosquitoes fly unaided; above their boundary layer their flight follows the track of the air in which they are flying [11]. Carriage on the wind for 176 km and 360 km was found for *Ae. sollicitans* and *Ae. vexans* respectively [12]. MacCreary and Stearns [13] caught *Cs. melanura* 13 km off land over Delaware Bay. These species of mosquito as well as *Cq. perturbans* have been caught at heights up to 30 m [12]. Mosquitoes are active between 13 °C and 35 °C and endurance was found to range from 12 to 22 h [12, 14]. Rosenberg and Magor [15] found flight times of 9–30 h for the brown planthopper in the East China Sea, and flight times up to 30 h might be expected with mosquitoes [1].

The principal virus cycle is between birds and *Cs. melanura*, and EEE virus is thought to spill over from that cycle to infect horses and man. EEE virus reaches a maximum titre in *Cs. melanura* at 7 days after infection, and the mosquito may be able to transmit the virus from 2–3 days after infection until the end of its life [16].

Weather data

The 6-hourly surface and 12-hourly 850 mb Northern Hemisphere maps of the Canadian Climate Centre and the daily surface Northern Hemisphere maps of the National Weather Center, USA were consulted for pressure, wind direction and speed, temperature, precipitation (rain) and fronts. Convergence and rain are associated with the passage of cold fronts and the convergence results in the concentration of insects [17]. Backward trajectories of winds were computed every 6 h up to 120 h (5 days), starting at three levels: 1000, 900 and 850 mb at approximate heights of 0·1, 1·0 and 1·5 km above sea level respectively as previously described [18]. Possible sources of mosquitoes were determined from the backward trajectories every 6 h up to 30 h to correspond with possible mosquito flight times [1].

ANALYSIS

EEE in USA, 1980–5

Table 1 lists the states east of a line from Texas to Illinois where EEE in horses might occur, together with the number of confirmed cases in horses for each year. There is likely to have been underreporting. Over 10 cases of EEE were diagnosed in Alabama in 1980, 1982 and 1983, in Florida in 1982–5, in Georgia in 1982, in Louisiana in 1981, in Michigan in 1980 and 1981, in New Jersey in 1984 and in Tennessee in 1983 [19–24, J. E. Pearson, personal communication, 1987].

Atlantic Coast outbreaks

The dates of the first outbreak in horses, the first isolation of EEE virus from mosquitoes and the first detection of EEE virus or antibody in birds were tabulated for Pocomoke Swamp, Delmarva (Delaware–Maryland–Virginia) Peninsula (1982 and 1983) and for New Jersey (1982–5) [25–32, W. J. Crans, personal communication, 1987, D. M. Watts, personal communication, 1988] (Table 2). In Table 2 the date in 1984 of the first isolation of Highlands J (HJ) virus is also given; HJ virus is a member of the WEE complex and has a similar epidemiology to EEE virus [6, 33]. In New Jersey in 1982 EEE infection was first detected in birds, then in mosquitoes and then in horses; in 1983 and 1985 disease in horses preceded isolation of virus from mosquitoes and in 1984 infection in mosquitoes and disease in horses occurred about the same time. In Pocomoke Swamp infection in birds and in mosquitoes occurred at the same time but was earlier in 1982 (early July) than in 1983 (late August). In 1982 EEE virus was isolated earlier from mosquitoes in Pocomoke Swamp than in New Jersey, but in 1983 isolation was at the same time for *Cs. melanura*.

An examination of the surface weather maps from 1982 to 1985 showed that the earliest days on which disease was observed, virus isolated or antibody detected (Table 2) were preceded by one or more days on which S to SW winds met cold fronts approaching from the northwest over New Jersey and the Delmarva

Table 1. *Eastern equine encephalitis in horses in United States by states, 1980–5*

	Year					
	1980	1981	1982	1983	1984	1985
Atlantic seaboard						
Maine (ME)	·	·	+	·	·	·
New Hampshire (NH)	+	·	+	·	·	·
Vermont (VT)	·	·	·	·	·	·
Massachusetts (MA)	·	·	+	·	+	·
Connecticut (CT)	·	·	·	+	+	·
Rhode Island (RI)	·	·	·	+	·	·
New York (NY)	·	·	+	+	·	·
New Jersey (NJ)	+	·	+	+	+	+
Pennsylvania (PA)	·	·	·	·	·	·
Delaware (DE)	·	·	·	+	·	·
Maryland (MD)	·	·	+	+	+	·
Virginia (VA)	·	·	+	·	+	·
North Carolina (NC)	·	+	+	+	+	+
South Carolina (SC)	+	+	+	·	+	+
Georgia (GA)	+	+	+	+	+	+
Florida (FL)	+	+	+	+	+	+
Gulf of Mexico, Mississippi Valley						
Michigan (MI)	+	+	+	+	·	·
Illinois (IL)	·	·	·	·	·	·
Indiana (IN)	+	+	·	+	·	·
Ohio (OH)	·	·	·	·	·	·
Missouri (MO)	·	·	·	·	·	·
Kentucky (KY)	·	·	·	·	·	·
West Virginia (WV)	·	·	·	·	·	·
Arkansas (AR)	·	·	·	·	·	·
Tennessee (TN)	·	·	·	+	·	·
Texas (TX)	·	+	·	·	+	·
Louisiana (LA)	·	+	+	+	+	·
Mississippi (MS)	+	+	+	+	+	+
Alabama (AL)	+	+	+	+	·	+

Table 2. *Dates of first isolation of eastern equine encephalitis or Highlands J viruses from mosquitoes or birds, development of antibody in birds and appearance of disease in horses in the Delmarva Peninsula and New Jersey, 1982–5*

Year	Place	Virus	Birds	Mosquitoes	Horses
1982	DMP*	EEE	7 July (antibody)	5 July *Cs. melanura*	—
	NJ	EEE	25 May (virus)	13 July *Cs. melanura* 4 August *Ae. sollicitans*	5 August
1983	DMP	EEE	Late August	29 August *Cs. melanura*	—
	NJ	EEE	—	Late August *Cs. melanura* 25 July *Cq. perturbans*	8 July (I)
1984	NJ	EEE	—	31 July (I) *Cs. melanura*	28 July (I)
		HJ	—	2 July *Cs. melanura*	
1985	NJ	EEE	—	19 August *Cs. melanura*	17 July (I)

* DMP, Delmarva Peninsula.

(I) Inland site in New Jersey; remainder in New Jersey are coastal sites.

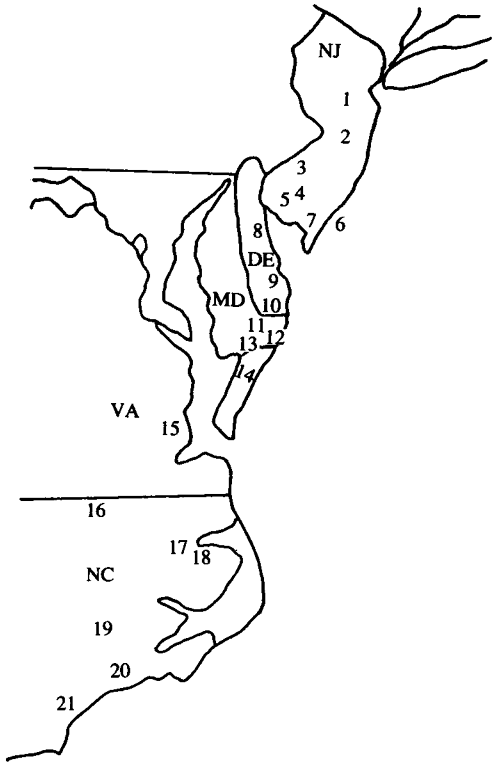

Fig. 1. Location map showing EEE outbreaks (1980–5) and possible sources. (1980): MI, Three Rivers (see Fig. 3); NJ, Gloucester Co. [3], Ocean City [6]; NY, Oneida Lake (see Fig. 3). (1982): MD, Pocomoke Swamp [13]; NJ, Dennisville [7]; NC, Kinston [19], Roanoke Rapids [16], Wilmington [21]; VA, Accomac [14], Williamsburg [15]. (1983): DE, Dover [8]; NJ, Jackson Township [2]; NC, Plymouth [18]; VA, Williamsburg [15]. (1984): DE, Georgetown [9], Selbyville [10]; MD, Pocomoke Swamp [13], Snow Hill [12]; NJ, Dennisville [7], Iona Lake [4], Monmouth Junction [1]. (1985): MD, Pocomoke Swamp [13], Salisbury [11]; NJ, Dennisville [7], Monroeville [5]; NC, Jacksonville [20], Williamston [17].

Peninsula. Backward trajectories of winds were computed starting at 18.00 h Greenwich Mean Time (GMT) (13.00 Eastern Standard Time, EST) for every 6 h up to 120 h for periods up to 15 days before disease, virus isolation or detection of antibody. Possible sources are given in Table 3 and locations are shown in Fig. 1. Backward trajectories for 1982 are shown in Fig. 2*a–d*. The 1000 mb trajectories indicate that North Carolina could have been the source for the Delmarva Peninsula within 8–18 h, and Delaware, Maryland, Virginia and North Carolina the sources for New Jersey within 4–24 h previously. The interval between arrival and disease in horses was 5–11 days, and between arrival and detection of virus or antibody 1–8 days. The temperatures were 13 °C or higher, and in 10 out of 11 instances arrival coincided with the passage of a cold front and rain and in one instance with rain.

The trajectories indicate that infection could have been carried on surface winds to the Delmarva Peninsula and to New Jersey either by mosquitoes or by birds. Since one of the birds from which EEE virus was isolated in 1982 in New

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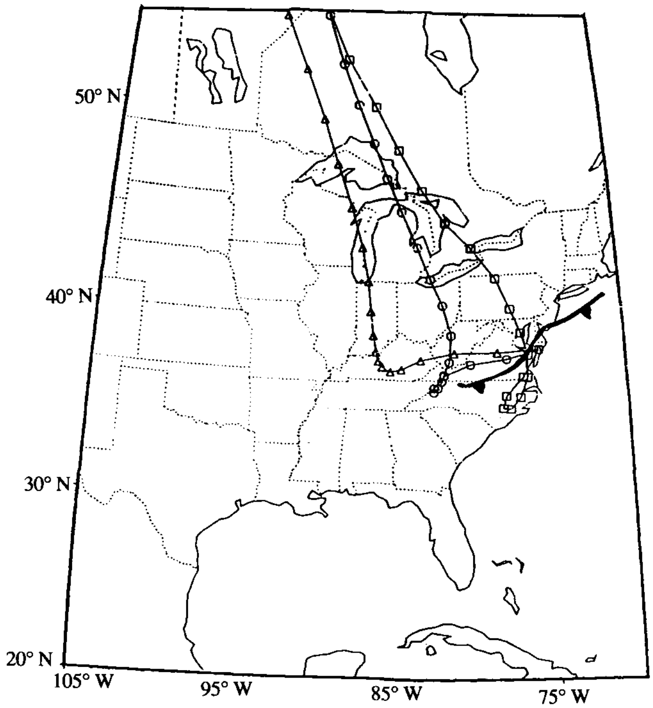

Fig. 2 (*a*).

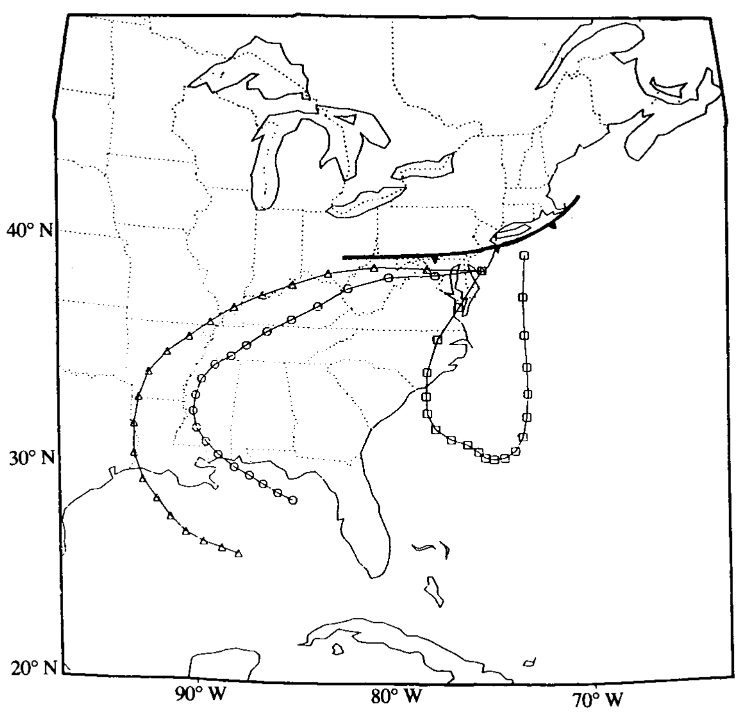

Fig. 2 (*b*).

Fig. 2. Fronts and 6-hourly segments of backward trajectories at three levels (△ 850 mb; ○ 900 mb; □ 1000 mb) terminating at: (*a*) Pocomoke Swamp, MD on 3 July 1982 at 18.00 GMT (13.00 EST); (*b*) Dennisville, NJ on 20 May 1982 at 18.00 GMT

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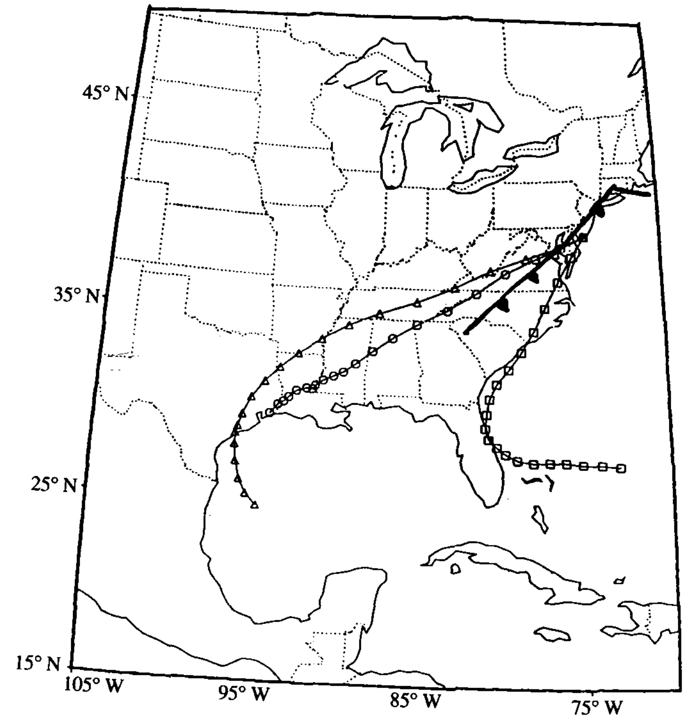

Fig. 2(*c*).

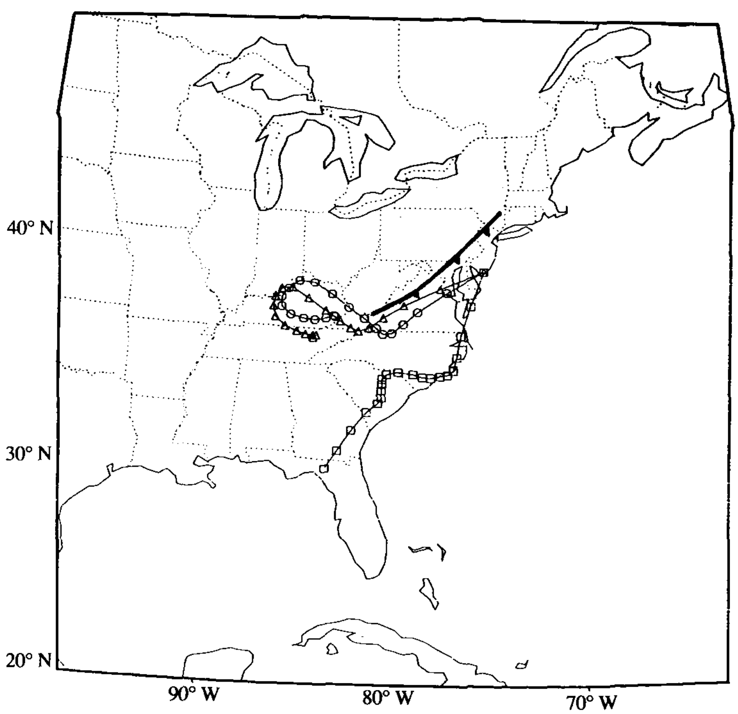

Fig. 2(*d*).

(13.00 EST); (*c*) Dennisville on 12 July 1982 at 18.00 GMT (13.00 EST); (*d*) Dennisville on 28 July 1982 at 18.00 GMT (13.00 EST).

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Table 3. *Source of backward trajectories at 1000 mb up to 24 h previously together with weather conditions on arrival for outbreaks of EEE in horses and virus isolations from mosquitoes and birds (Atlantic Coast)*

Location, date of disease, etc.	Date of arrival	Source at 1000 mb, 4–24 h before	Interval (days)	Conditions
	1982			
Pocomoke Swamp, MD *Cs. melanura* virus 5 July 1982 (Fig. 2*a*)	29 June 1982	9* Plymouth, NC	6	TFR†
	3 July 1982	8 Roanoke Rapids, NC	2	TFR
		18 Kinston, NC		
Dennisville, NJ, bird virus 25 May 1982 (Fig. 2*b*)	20 May 1982	4 Pocomoke, MD	5	TFR
		22 Wilmington, NC		
Dennisville, NJ *Cs. melanura* virus 13 July 1982 (Fig. 2*c*)	12 July 1982	6 Pocomoke, MD	1	TFR
		12 Williamsburg, VA		
Dennisville, NJ *Ae. sollicitans* virus 4 August 1982 (Fig. 2*d*)	28 July 1982	6 Accomac, VA	7	TFR
	1983			
Jackson Township, NJ horse 8 July 1983	28 June 1983	12 Dover, DE	10	TFR
		18 Williamsburg, VA		
		24 Plymouth, NC		
	1984			
Iona Lake, NJ *Cs. melanura* virus 31 July 1984	27 July 1984	6 Snow Hill, MD	4	TFR
Monmouth Junction, NJ horse 28 July 1984	18 July 1984	6 Pocomoke, MD	10	TFR
	23 July 1984	12 Selbyville, DE	5	TR
	1985			
Monroeville, NJ horse 17 July 1985	6 July 1985	6 Salisbury, MD	11	TFR
		18 Williamston, NC		
		24 Jacksonville, NC		
Dennisville, NJ *Cs. melanura* virus 19 August 1985	15 August 1985	6 Pocomoke, MD	4	TFR

* Source 9 h previously.
† T, temperature ⩾ 13 °C, F, cold front, R, rain.

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Jersey [26] was a permanent resident, it seems likely that the introduction would have been by infected mosquitoes, which on arrival fed on birds. The *Cs. melanura*, from which virus was isolated on 13 July 1982 in New Jersey, could have come from the Delmarva Peninsula (Fig. 2*b*).

Cs. melanura is also the principal vector of Highlands J (HJ) virus, which infects birds and like EEE virus has been isolated from birds and mosquitoes along the Atlantic Coast [33]. In the Delmarva Peninsula and in New Jersey HJ virus has been isolated from *Cs. melanura*, in some years before, in some years at the same time and in other years after EEE virus depending on the site [34–37]. Backward trajectories were computed for a period before the first isolation of HJ virus from *Cs. melanura* at Dennisville on 2 July 1984 [W. J. Crans, personal communication, 1987]. The trajectory showed a source at Georgetown, Delaware 6 h before arrival on 1 July 1984; arrival was accompanied by the passage of a cold front and rain.

EEE has occurred in upstate New York on many occasions [38, 39]. In 1980 at Oneida Lake EEE virus was first isolated from *Cs. melanura* on 16 September [38]. Backward trajectories indicated a possible source on 14 September in Gloucester County, New Jersey 16 h previously. On 17 September 1980 backward trajectories showed that Ocean City, New Jersey could have been the source 12 h previously; on that day an increase in the *Cs. melanura* caught at Oneida Lake was found. Arrivals coincided with the passage of a cold front and rain. Surface winds could have carried *Cs. melanura* mosquitoes infected with EEE virus from New Jersey to upstate New York. The backward trajectories computed for the Delmarva Peninsula, New Jersey and upstate New York indicate that there could be a series of flights of infected mosquitoes from North Carolina in stages during late spring and summer to upstate New York, the mosquitoes landing at points of convergence, where warm southerly winds meet cold fronts advancing from the northwest.

Michigan outbreaks

In 1980 there was an epidemic of EEE in Michigan affecting horses, man and pheasants. The first cases in horses were reported at the end of June and on 24 July [40, 41].

Days up to 16 days before the first outbreaks were chosen for computation of backward trajectories. The outbreak at the end of June could have had a source on the boundary between southern Indiana and western Kentucky on 14 June (18 h previously) or on 23 June (24 h previously). The outbreak on 24 July could have come from western Kentucky on 15 July (24 h previously) or on 20 July (18 h previously). Surface winds were involved, and the arrival of the infected mosquitoes would have coincided with the passage of a cold front and rain on 14 June, 15 July and 20 July. Temperatures were higher than 13 °C. The interval between arrival of mosquitoes and disease in horses was 4 or 9 days for the outbreak on 24 July.

DISCUSSION

Reeves [42] and Rosen [43] discussed overwintering of arboviruses under adverse conditions. EEE virus has been found experimentally to survive in snakes and frogs and in birds [2, 42]. In the field EEE virus was isolated from a white-footed mouse during winter in New Jersey [Goldfield and Sussman, 1964, quoted by 2]. Survival of EEE virus in vertebrates is a possibility, but quantitative data are lacking [2].

In support of transovarial transmission Schaeffer and Arnold [44] and Chamberlain, Sikes and Nelson [45] recovered EEE virus from egg rafts deposited by infected *Cq. perturbans*; Hayes and colleagues [46] isolated EEE virus from *Cs. melanura* larvae collected in Massachusetts, and Chamberlain and Sudia [47] isolated virus from a pool of *Cs. melanura* males in Alabama. However, in field studies on *Cs. melanura*, *Cq. perturbans* and *Ae. cantator*, workers in Maryland, New Jersey and New York failed to isolate EEE virus from larvae, adults reared from larvae, or male mosquitoes [25, 29, 39, 48, 49]. In experimentally infected *Cs. melanura* the ovarioles remained free of virus [16].

EEE virus is regularly isolated from birds, and virus could be re-introduced to an area by migratory birds in the spring [2]. Calisher and co-workers [50] isolated a South American strain of virus from migratory birds entering the United States via the Gulf of Mexico. The backward trajectories indicate that winds are available to assist bird flight from the Gulf Coast to Michigan or to the Delmarva Peninsula or from Georgia northwards along the Atlantic Coast (Fig. 2). Based on wind speed and uninterrupted flight the distance would be covered in 2·5–4 days, a period within the duration of the bird's viraemia. In 1982 in New Jersey the first isolation of EEE virus was from birds on 25 May [26]. One of the species was resident, and thus birds were unlikely to have introduced the virus on the trajectory arriving on 20 May. In 1980 in New Jersey antibody to EEE virus was detected in juvenile birds in late June before virus was first isolated from *Cs. melanura* in late July [34]. Chamberlain [2] indicated that EEE virus was usually isolated some time after the peak of bird migration. Thus if birds introduce virus in the spring, the virus must cycle at a level difficult to detect between birds and mosquitoes before amplification or entry into the main mosquito–bird cycle later in the year. EEE virus has been isolated from birds migrating from the north to the southern United States in the autumn, and their migration has been associated with the passage of cold fronts [51].

Another possibility is the introduction of virus by infected mosquitoes carried on the wind, the analysis of which has been the subject of this paper.

The findings are preliminary, but indicate that there were backward trajectories of winds within acceptable periods before the isolation of EEE or HJ virus from *Cs. melanura*, *Ae. sollicitans* or birds and before disease in horses. These winds could have led to the introduction of infected mosquitoes. The backward trajectories at 1000 mb provide origins, where EEE virus was or could have been circulating, within a flight time of up to 24 h (flight endurance). As before [1], in most instances 18.00 GMT (13.00 EST) was taken as the time of arrival. Interpolation for different arrival times and for flight at different heights could be undertaken in order to determine the source and time of arrival more exactly.

The trajectory analyses for the Delmarva Peninsula, New Jersey and upstate New York suggest that there could be a sequence of carriage of infected mosquitoes on the wind from North Carolina northwards along the Atlantic seaboard. The variation in the times of the first isolation of virus or of the first appearance of disease in horses (Table 2) could result from the variation in the location where mosquitoes infected with EEE (or HJ) viruses land, due to the

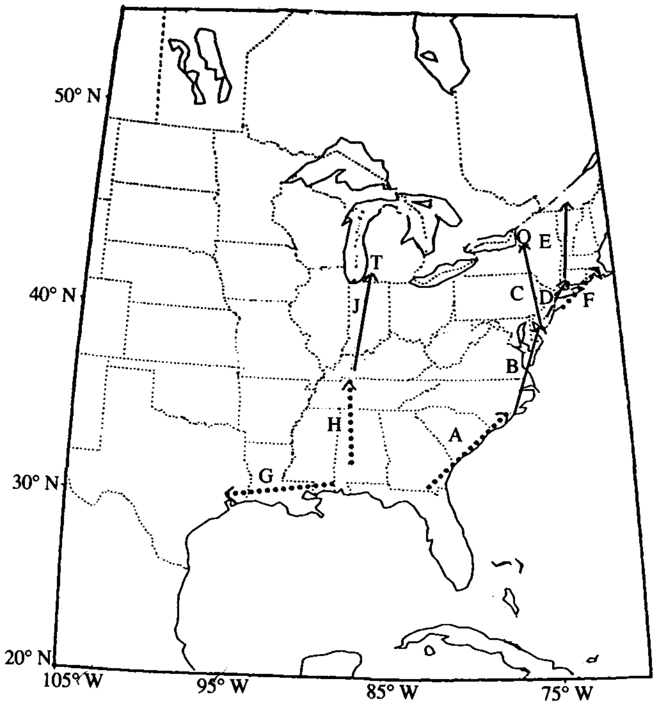

Fig. 3. Suggested spread of EEE in North America. ←—, Spread based on trajectories; ←...., possible spread. A, Florida, Georgia to North Carolina; B, North Carolina to Delmarva Peninsula and New Jersey; C, New Jersey to upstate New York; D, New Jersey to Connecticut; E, Connecticut to Quebec; F, New Jersey to Massachusetts and Rhode Island; G, Florida, Alabama to Louisiana and Texas; H, Alabama to Kentucky; J, Kentucky to Michigan; O, Oneida Lake, New York; T, Three Rivers, Michigan.

convergence of southerly winds with cold fronts associated with rain. In 1983 and 1985 the first arrivals of infected mosquitoes could have been at inland sites in New Jersey; in 1984 arrivals at inland sites and at coastal sites could have been almost simultaneous. In New Jersey in 1982 EEE virus was first isolated from birds at the end of May. It was pointed out that if winds were responsible, introduction would have been by mosquitoes rather than birds. The backward trajectory analysis showed Pocomoke Swamp as a possible source 4 h previously; however, EEE virus was not detected in Pocomoke Swamp until early July. A further possible source was the Atlantic Coast of North Carolina at Wilmington. This gave a flight time of 22 h, which is within the endurance of mosquitoes [14]. The winds on 19–20 May would have carried mosquitoes northwards until the meeting with the cold front led to the landing of the mosquitoes. This type of anomaly of virus infection appearing in northern areas earlier than further south was found with WEE and was attributed to carriage of *Cx. tarsalis* mosquitoes on warm winds until they met cold fronts [1]. Thus the mosquitoes would have overflown intermediate areas. Such introductions might be abortive if conditions for maintenance of infection (sufficient local mosquitoes and hosts) are not present early in the year. The mosquito most likely to be involved is *Cs. melanura*, which transmits both EEE and HJ viruses and which will bite horses as well as birds [8].

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However, introduction as well as amplification of infection could be by *Cq. perturbans* at inland sites and *Ae. sollicitans* at coastal sites [27, 29].

Michigan experienced epidemics of EEE in 1941 and 1973 as well as in 1980. *Cq. perturbans* was associated with the outbreaks in 1973 and 1980 [52, D. B. Francy quoted by 6] and could have been responsible for introducing EEE virus from further south in the Mississippi Valley in southern Indiana, western Kentucky and western Tennessee. The distribution of *Cs. melanura* extends to the west of the Mississippi [33], and EEE virus has been isolated from *Cs. melanura* as well as from *Cq. perturbans* in Michigan [53]. Thus EEE virus could have been introduced by infected *Cs. melanura*.

In the southern states (Florida, Georgia, Alabama, Mississippi and South Carolina) *Cs. melanura* and other mosquitoes are able to breed all the year [33, 54]. In Florida EEE virus has been isolated and EEE seen in horses every month of the year [24, 55, 56]. Thus in these states EEE virus could be maintained in a vertebrate host–mosquito cycle and be a source of virus to other areas. Examination of weather maps indicated that in the periods before the dates of the suggested flights in 1980–5 there were winds blowing from these states, which could have carried infected mosquitoes to North Carolina and Virginia along the Atlantic Coast and to western Tennessee and Kentucky along the Mississippi Valley.

It is suggested that there is a continual cycle of EEE virus in birds and mosquitoes in south-eastern USA. From there virus could be carried north-eastwards along the Atlantic Coast, northwards up the Mississippi Valley and westwards to Louisiana and Texas (Fig. 3). The possibility of an epidemic occurring would depend on: (i) presence of EEE virus cycle in mosquitoes and birds at source, (ii) suitable winds to carry infected mosquitoes with the potential for biting horses to areas where convergence and hence concentration of mosquitoes can occur, and (iii) sufficient mosquitoes and susceptible hosts at the place of landing to maintain infection. At the fringes of the range of EEE as in New York, New England, Quebec and Michigan the variable occurrence of outbreaks could be due among other factors to the variation in areas where cold fronts meet warm southerly winds.

Further investigations could be directed to study of the carriage of infected mosquitoes on the wind through measurement of insect dispersion and movement by radar, by sampling of mosquitoes at various heights by aerial samplers mounted on helicopters and by molecular characterization of virus isolates [57, 58].

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