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Impact of climate on western equine encephalitis in Manitoba, Minnesota and North Dakota, 1980–1983

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SUMMARY

Information was collected on confirmed outbreaks of western equine encephalitis (WEE) in North America east of the Rockies for 1981 and 1983 (epidemic years) and 1980 and 1982 (non-epidemic years). The initial pattern of outbreaks in Manitoba, Minnesota and North Dakota was determined for each year. Backward (and in some instances forward) wind trajectories were computed for each day 4–15 days (incubation period) before the initial outbreaks of WEE in a given area of province or state.

During these years the timing and location of WEE outbreaks in horses and man, seroconversion in chickens, the maximum *Culex tarsalis* counts at Winnipeg and first isolation of WEE virus from *C. tarsalis* could be correlated with trajectories of winds from states further south within acceptable intervals. It is suggested that *C. tarsalis* mosquitoes infected with WEE virus are carried on the wind from Texas on the Gulf of Mexico, where they continue to breed during the northern winter months, to northern Texas and Oklahoma in the spring. In May, June and July *C. tarsalis* are carried north on southerly winds from these states through Kansas and Nebraska to North Dakota, Minnesota, Wisconsin and Manitoba. Distances of 1250–1350 km are traversed in 18–24 h at heights up to 1·5 km with temperatures $\geqslant$ 13 °C. Landing takes place where the warm southerly winds meet cold fronts associated with rain. Convergence leads to concentration of *C. tarsalis* and determines where outbreaks occur. It is possible that return of new generations of *C. tarsalis* to the south may occur later in the year.

The development of an epidemic of WEE in the northern states and provinces would appear to depend on (i) suitable trajectories from the south in June and July with temperatures $\geqslant$ 13 °C meeting cold fronts with rain, (ii) sufficient *C. tarsalis* infected with WEE virus at source, carried on the wind and locally, (iii) *C. tarsalis* biting horses and man, (iv) maintenance of local mosquito populations in August and (v) susceptible hosts (birds) at source and susceptible hosts (horses and man) locally.

Possible methods of prediction involving determination of trajectories,

identification of *C. tarsalis* blood meals, measuring seroconversion in calves are discussed in addition to the methods already in use.

INTRODUCTION

Western equine encephalitis has been recognized in the prairie provinces of Canada (Manitoba, Saskatchewan and Alberta) and in Minnesota and North Dakota in USA since 1935 (Artsob & Spence, 1979; Eklund, 1946; Brust, 1982*a*; Grimstad, 1983). The most recent epidemic years were 1975, 1977, 1981 and 1983 (Sekla, 1982; Neufeld, 1984). WEE is regarded as endemic in these provinces and states, but the factors influencing the overwintering of the virus and the development of the epidemics are not clearly defined. Overwintering of WEE virus in hosts such as amphibians, reptiles, birds and small mammals or in mosquito vectors in surviving adults or eggs has been suggested, but others consider that the virus is reintroduced annually in the spring by migrating birds from further south (Hayes & Wallis, 1977; Chamberlain, 1980; Neufeld, 1982; Walton, 1981). A further possibility is that WEE virus is introduced by carriage on the wind of infected mosquitoes (Sellers, 1980).

To examine this possibility, wind trajectories for 1980–83 were analysed in relation to the location and time of WEE outbreaks in Manitoba, Minnesota and North Dakota and in other places during those years. The analysis is presented in the paper and hypotheses are suggested to account for the findings.

CONSIDERATIONS

Virus

The WEE viruses isolated during 1980–83 are regarded as being western variants of the WEE complex. Trent & Grant (1980) determined the relationships of a number of isolates from North America up to 1975 by immunochemical and oligonucleotide fingerprint techniques.

The virus cycles between vertebrate hosts – small mammals, birds, reptiles and amphibians (horses and man are regarded as dead-end hosts) and mosquito vectors including *C. tarsalis*, *Culiseta inornata* and *Aedes* species.

Hosts

In horses and man the period between infection with WEE virus and the time disease is seen or the sample received in the laboratory is considered to be 4–15 days (Calisher *et al.* 1983). Fever may occur on the first day after infection. Viraemia is found in horses between the first and fifth day after infection, but experimentally the titre failed to attain that required to infect *C. tarsalis* (Sponseller *et al.* 1966). In birds virus is present in blood between the first and fifth days at titres often sufficient to infect mosquitoes (Holden *et al.* 1973). Viraemia also occurs in small mammals such as Richardson's ground squirrels (Leung *et al.* 1976). Haemagglutination inhibition (HI) antibodies develop in sentinel chickens between the sixth and fourteenth day after infection (Wong, Lillie & Drysdale, 1976).

Vectors

The main vector of WEE virus is *C. tarsalis*. Other vectors implicated in transmission are *Cu. inornata*, *Ae. vexans* and virus has been isolated from *Ae. campestris*, *Ae. flavescens*, *Ae. spencerii*, *Ae. melanimon*, *Anopheles earlei* and other species (McLintock *et al* 1970; Sekla & Stackiw, 1982; Grimstad, 1983).

C. tarsalis, *Cu. inornata* and *An. earlei* overwinter in northern USA and Canada as non blood-fed adults; *Aedes* species overwinter as eggs. Further south in Texas and California adults of some of these species have been caught every month from September to April (Eads, 1965; Meyer, Washino & McKenzie, 1982).

Aedes species and *Cu. inornata* feed mainly on mammal blood. *C. tarsalis* has been found to feed on birds early in the season, changing later in the year to feed on both birds and mammals (Tempelis, 1975).

The mosquito species such as *C. tarsalis* responsible for transmitting WEE virus lay eggs 2–3 days after taking a blood meal and feed again 1–2 days later. This pattern continues throughout their life. Under optimum conditions the period from the egg stage to adult could take 7–10 days. The adult takes a blood meal 3 days after emerging, at which time it could become infected with WEE virus. The virus develops in the mosquito and the mosquito can transmit the virus after 6 days and every 3–4 days when taking blood meals till the end of the mosquito's life (Henderson, Brust & Wong, 1979). With a survival rate of 0·77, 1% of the original mosquito population would be alive 17 days later (Grimstad, 1983).

Mosquito flight

The flight speeds of *C. tarsalis*, *Cu. inornata* and *Ae. vexans* lie between 1·3 and 2 m s^{-1} (Johnson, 1969). Thus at wind speeds greater than 3 m s^{-1} (10·8 km h^{-1}) the track of the mosquito would be that of the air in which it is flying. Dispersal of 16 km per night was recorded for *C. tarsalis*, *Ae. vexans* travelled up to 360 km in association with a cold front and *Cu. inornata* has been caught 10 km from its breeding area (Mitchell, Francy & Monath, 1980; Johnson, 1969; Hudson & Edman, 1978). *C. tarsalis* has been caught at heights up to 615 m by day and by night, *Ae. vexans* up to 1500 m and *Cu. inornata* at 30 m (Johnson, 1969).

Climatic factors affection mosquitoes

Mosquitoes are affected by temperature and moisture. Increase in temperature leads to the development from egg to adult; moisture affects the provision of breeding sites. Mosquitoes such as *C. tarsalis* are active between 13 °C and 35 °C and temperatures in this range are found at heights up to 1·5 km or even higher. Thus flight may occur up to these heights.

Convergence and rain (precipitation) are usually associated with cold front passage. Convergence at such fronts results in the concentration of the insects (Rainey, 1983). Insects are affected by the drop in temperature and descend in the downdraughts. Wind speeds up to 40 km h^{-1} are found, but with low level jets, speeds may be as high as 90 km h^{-1} at temperatures within the activity range of insects.

Endurance of mosquitoes was determined for various species and ranged from up to 12 to 22 h (Johnson, 1969). Rosenberg and Magor (1983) carried out a trajectory analysis on the flight duration of the brown planthopper, whose flight speed is estimated to be 1–2 m s^{-1}. They found that in the East China Sea flight times between sources and ships ranged from about 9 to 30 h. By analogy it would be reasonable to suppose that flight times in mosquitoes could be as long as 30 h.

Thus with wind speeds from 20 km h^{-1} to 90 km h^{-1} and endurance of 10–30 h a mosquito could be carried on the wind from 200 to 2700 km before landing.

Sources of information

Manitoba. Information on outbreaks of WEE in horses, disease in man, seroconversion in chickens and mosquito catches was obtained from Brust (1982*b*), Sekla (1982), Sekla & Eadie (1984), Raddatz (1986), Neufeld (1982, 1984 and personal communications 1986, 1987) and Nayar, G. P. S. (personal communication, 1987).

Minnesota and North Dakota. Location and dates of outbreaks were provided by Ives, S. (personal communications, 1987) on Minnesota and Holmes, S. E. (personal communications, 1987; North Dakota State Department of Health, 1981) on North Dakota.

USA. Details of the month and state from which samples positive for WEE infection were obtained, were supplied by J. E. Pearson (1983, 1984 and personal communications 1986, 1987).

Colorado, Illinois, Iowa, Montana, Oklahoma and Wisconsin. Reports on outbreaks in 1981 were received from all these states (Pape, J., Doby, P. B., Schmall, L. M., James, D. O., Eskew, G. & Arnoldi, J. M., personal communications 1987).

Climatic data. Data on temperature and precipitation (rain) were obtained from the records of the Canadian Climate Centre.

The 6-hourly surface and 12-hourly 850 mb Northern Hemisphere maps of the Canadian Climate Centre and daily surface Northern Hemisphere map of the National Weather Center, USA were consulted for pressure, wind direction and speed, temperature, precipitation and fronts.

Trajectory analysis. 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. These heights vary along the trajectory depending on the position of the air parcel. A three-dimensional trajectory model (Olson, Oikawa & Macafee, 1978) was applied. The model uses objectively analysed wind fields at four standard pressure levels (1000, 850, 700 and 500 mb) on the Canadian Meteorological Centre grid of 381 km. Cubic interpolation is used to obtain winds at intermediate levels in the vertical, and bilinear interpolation between grid points in the horizontal. Heights and temperature fields are used to compute vertical motion at the upper levels. Mountain- and friction-induced vertical motion are computed at the lowest level. Trajectory 6-h segment endpoints are determined using an iterative scheme on the three-dimensional wind field until horizontal and vertical convergence criteria are reached.

Forward trajectories were similarly computed every 6 h up to 48 h (2 days).

Possible sources of mosquitoes were determined from the backward trajectories to correspond with flight times of 18, 24 and 30 h.

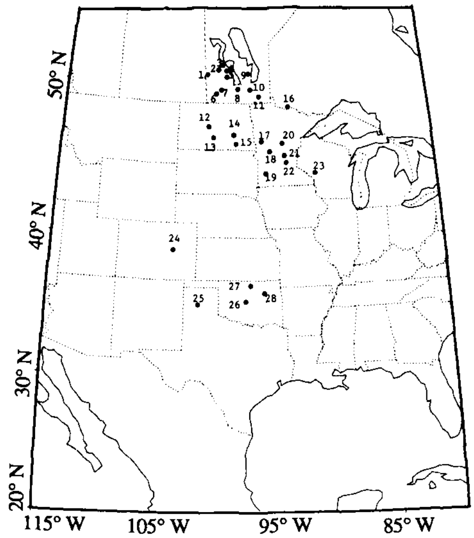

Fig. 1. Location map of North America showing WEE outbreaks (1980–83) selected for trajectory analysis.

1980	Manitoba	Dauphin (2)	1982	Manitoba	Ste. Rose du Lac (4)
		Rorketon (3)			Portage la Prairie (8)
	Minnesota	Benton (22)			Arborg (9)
1981	Manitoba	Russell (1)		Minnesota	Alexandria (18)
		Brandon (7)	1983	Manitoba	McCreary (5)
		Winnipeg (10)			Dauphin (2)
	W. Ontario	Fort Frances (16)			Winnipeg (10)
	Wisconsin	Blair (23)			Marchand (11)
	Minnesota	Marshall (19)			Souris (6)
		Buffalo (21)		Minnesota	Pelican Rapids (17)
	North Dakota	Underwood (12)			Brainerd (20)
		Berlin (15)		North Dakota	Bismarck (13)
	Colorado	Simla (24)			Jamestown (14)
	Oklahoma	Tonkawa (27)			
		Oklahoma City (26)			
		Tulsa (28)			
	Texas	Amarillo (25)			

ANALYSIS

The outbreaks for each year were plotted by location and date. Minnesota and North Dakota were divided into east and west to correspond with Manitoba's eastern and western boundaries. Manitoba was also divided into east and west at Portage la Prairie. Outbreaks in May, June, July and the beginning of August which were unique or representative of the first outbreaks in the different areas or states were selected for trajectory analysis (Fig. 1).

Disease in horses and man was considered to have occurred 4–15 days after arrival of the mosquito. In analysis of the development of an epidemic further outbreaks of disease would be seen 8–19 days after arrival if mosquitoes bit for the second time and 12–23 days after arrival where local mosquitoes became involved in transmission.

Table 1. *Number of confirmed outbreaks of WEE in horses in USA, Minnesota, North Dakota and Manitoba, 1980–83*

Year	1980	1981	1982	1983
USA	27	328	27	77
Minnesota	1	40	3	13
North Dakota	0	58	0	16
Manitoba	2	133	3	24

Table 2. *Confirmed outbreaks of WEE in horses by province or state, North America (east of the Rockies), May–August, 1980–83*

	Year and month															
	1980				1981				1982				1983			
Province or State	M	J	J	A	M	J	J	A	M	J	J	A	M	J	J	A
Manitoba/W. Ontario	1†	0	0	1	0	1	44	73	0	0	2	1	0	1	0	19
Montana		——NR——			—	1	9	14		——NR——			—	—	—	3
North Dakota		——NR——			1	0	42	15		——NR——			0	0	6	10
Minnesota	1	0	0	0	0	0	23	13	0	0	1	1	0	0	3	7
Wyoming		——NR——			—	—	—	4	—	—	—	1		——NR——		
South Dakota		——NR——			—	—	11	20	—	—	—	2	—	—	1	9
Nebraska	—	—	1	—	—	—	10	13		——NR——			—	—	—	2
Iowa		——NR——			—	—	1	8		——NR——				——NR——		
Wisconsin		——NR——			—	1	2	—		——NR——				——NR——		
Colorado		——(7)——				——(67)——				——(17)——				——(15)——		
Kansas		——NR——			—	—	2	4	—	—	—	1	—	—	1	3
Oklahoma		——NR——			—	2	4	5		——NR——				——NR——		

* M, J, J, A, May, June, July, August. NR, not recorded.
† No. of outbreaks. (7), Total for year.

Table 3. *Outbreaks of WEE in horses by periods of 7–8 days in July 1981 and in July–August 1983 in Minnesota, North Dakota and Manitoba*

	W. North Dakota	E. North Dakota, W. Minnesota	Manitoba	E. Minnesota
1981*				
1–8 July	0	2	0	5
9–16 July	2	9	2	4
17–24 July	5	10	8	1
25–31 July	3	20	35	4
1983				
17–24 July	0	2	0	0
25–31 July	0	6	0	0
1–8 August	1	2	3	0
9–16 August	0	1	4	3

* First outbreaks in horses: N. Dakota, 25 May 1981; W. Ontario, 22 June 1981. First outbreaks in man: Manitoba W., 7 July 1981; Manitoba, E., 13 July 1981.

Western equine encephalitis 1980–83

There were more outbreaks of WEE in Manitoba, Minnesota and North Dakota as well as in USA in 1981 and 1983 than there were in 1980 and 1982 (Table 1).

In 1981 and 1983 confirmed cases of WEE were found in May and June. In 1981 the majority of cases was in July, but in 1983 most cases occurred in August (Table 2). In 1980 some cases occurred in May but few later in the year. In 1982 cases did not appear until July and August (Table 2).

In 1981 apart from the single outbreaks in North Dakota on 25 May and W. Ontario on 22 June, the start of the epidemic was first seen in eastern North Dakota and in Minnesota and then in Manitoba and western North Dakota (Table 3). In 1983 apart from the single outbreak in Manitoba in June, disease was seen in eastern North Dakota and western Minnesota 2–3 weeks before being seen in western North Dakota, eastern Minnesota and Manitoba (Table 3).

In 1981 in Manitoba disease in horses, disease in man and seroconversion in chickens occurred about the same time and also could be correlated with the rise in *C. tarsalis* caught in Winnipeg and first isolation of WEE virus from *C. tarsalis* (Table 4). In 1983 seroconversion in chickens, rise in *C. tarsalis* count and isolation of virus preceded the main epidemic in horses in August, which in turn was before the first case in man (Table 4).

Between 1980 and 1983 there was little correlation between the number of cases in horses and the peak weekly mean daily count of *C. tarsalis* in Winnipeg (Table 4).

Trajectories

1981. In Table 5 the analysis of trajectories in 1981 indicates that backward trajectories to the south to South Dakota, Nebraska, Kansas, Oklahoma and Texas as the main sources could be found for each case examined. Forward trajectories from Amarillo, Texas, Oklahoma City and Tulsa, Oklahoma for May and June confirmed the findings, i.e. arrival within 30 h at sites where disease was subsequently observed (Fig. 2*a*–*g*, backward trajectories; *h*, forward trajectory).

Table 4. *Dates of early appearance in Manitoba of WEE in horses and man, seroconversion in chickens, peak of* C. tarsalis *count at Winnipeg and isolation of virus*

Year	Disease in horses	Disease in man	Seroconversion in chickens	Maximum count of *C. tarsalis* at Winnipeg (mean daily)	Isolation of WEE virus from *C. tarsalis*
1980	27 May (W) (*a*) (2) (*b*)	—	Before 11 June (W) 17 June W) (3·3 %) (*c*)	28 July (5) (d)	—
1981	22 June (O) 14 July (W) 21 July (E) (133)	7 July (W) 13 July (E) (25) (*b*)	14 July (E) (84 %)	8 July (60)	6 July (E)
1982	6 July (W) 28 July (W) (3)	—	—	28 July (90)	—
1983	17 June (W) 2 August (E) (24)	12 August (18)	Before 29 June (EW) (47 %)	18 June (425)	13 July (E)

(*a*) W = Western Manitoba, E = Eastern Manitoba, O = Western Ontario. (*b*) Total No. of outbreaks in horses or man. (*c*) Percentage seroconversion for year in chickens. (*d*) Highest mean daily count of *C. tarsalis*.

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Table 5. *Source of backward trajectories at 850, 900, and 1000 mb 18, 24 and 30 h previously, together with climate conditions on arrival for outbreaks of WEE in horses and man, seroconversion in chickens, maximum* C. tarsalis *counts* and virus isolation in 1981*

Location date of diseases etc.	Date of arrival	Source at mb† 850	900	1000	Interval (days)	Conditions‡
Underwood, ND	21 May	18 Col. (E)	Kan. (W)	Kan. (W)	4	TFR
25 May	1981	24 Okl.	Okl.	Okl.		
horse (Fig. 2*a*)		30 Tex.	Tex.	Tex.		
Ft. Frances, Ont.	14 June	18 Min. (E)	Wis. (W)	Wis. (N)	8	TFR
22 June	1981	24 Iowa (W)	Iowa (W)	Wis. (C)		
horse (Fig. 2*b*)		30 Kan. (NE)	Mis. (N)	Wis. (C)		
		36 Okl.	Mis. (S)	Ill.		
Blair, Wis.	14 June	18 Okl. (E)	Okl. (E)	Ark. (C)		TFR
June	1981	24 Tex. (C)	Tex. (C)	Lou. (N)		
horse		30 Tex. (S)	Gulf	Lou. (3)		
Tonkawa, Okl.	15 June	18 Tex. (SE)	Tex. (SE)	Tex. (SE)	10	TFR
25 June	1981					
horse						
Simla, Col.	25 June	18	Kan. (SE)		10	TR
30 June	1981	24	Tex. (NW)			
horse (Fig. 2*c*)		30	Tex. (NW)			
Buffalo, Min.	28 June	18 Kan. (C)	Kan. (C)	Mis. (S)	6	TFR
4 July	1981	24 Okl. (W)	Okl. (W)	Ark. (N)		
horse (Fig. 2*e*)		30 Tex. (NW)	Tex. (NW)	Ark. (N)		
Marshall, Min.	27 June	18 Kan. (S)	Kan. (S)	Mis. (W)	9	TFR
6 July	1981	24 Okl. (N)	Okl. (C)	Mis. (W)		
horse		30 Okl. (C)	Okl. (C)	Mis. (W)		
Berlin, ND	27 June	18 Neb. (S)	Neb. (S)	Kan. (N)	11	TFR
8 July	1981	24 Col. (E)	Kan. (W)	Kan. (S)		
horse (Fig. 2*d*)		30 Okl. (W)	Okl. (W)	Okl. (W)		

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Table 5. (*cont.*)

Location date of diseases etc.	Date of arrival	Source at mb† 850	900	1000	Interval (days)	Conditions‡
Russell, Man.	1 July	18 SD (S)	SD (S)	SD (S)	M 6§	TFR
7 July man	1981	24 Neb. (C)	Neb. (C)	Neb. (C)	H 13	
14 July horse		30 Neb. (C)	Neb. (C)	Neb. (C)		
(Fig. 2*f*)	6 July 1981	18 SD (W)	SD (W)	SD (W)	H 8	TFR
Brandon, Man.	11 July	18 ND (E)	ND (E)	Man. (S)	H 6, 11	TFR
17/22 July horse	1981	24 ND (S)	ND (S)	Man. (S)	Ch. 13	
24 July chicken		30 SD (3)	SD (E)	Man. (S)		
Winnipeg, Man.	2 July	18 ND (W)	ND (W)	SD (C)	M 11	TFR
13 July man	1981	24 Mon. (SE)	SD (W)	Neb. (NE)	Ch. 12	
14 July chicken		30 Wyo. (NE)	Neb. (W)	Neb. (SE)	Virus 4	
6 July virus					Mosq. 6	
8 July *C. tarsalis*						
(Fig. 2*g*)	7 July	18 Neb. (N)	Neb. (N)	Ohio (W)	M 6	TR
	1981	24 Neb. (S)	Neb. (S)	Ohio (S)	Ch. 8	
21 July horse	11 July	18 ND (E)	Min. (NE)		10	TFR
	1981	24 ND (S)	Min. (NE)			

* Maximum *C. tarsalis* count – date of maximum weekly mean daily *C. tarsalis* counts from Raddatz (1986).

† Provinces and States. Ark., Arkansas; Col., Colorado; Ill., Illinois; Kan., Kansas; Lou., Louisiana; Man., Manitoba; Min., Minnesota; Mis., Missouri; Mon., Montana; Neb., Nebraska; ND, North Dakota; Ohio; Okla., Oklahoma; Ont., Ontario; SD, South Dakota; Tex., Texas; Wis. Wisconsin; Wyo., Wyoming; (E), (N), (S), (W), (C), East, north, south, west, central. (18, 24, 30-time before (h).)

‡ Conditions. T, temperatures up to 1·5 km. above 13 °C; R, rain; F, cold front.

§ M., Man; H., Horse; Ch., Chicken; Mosq., Mosquito.

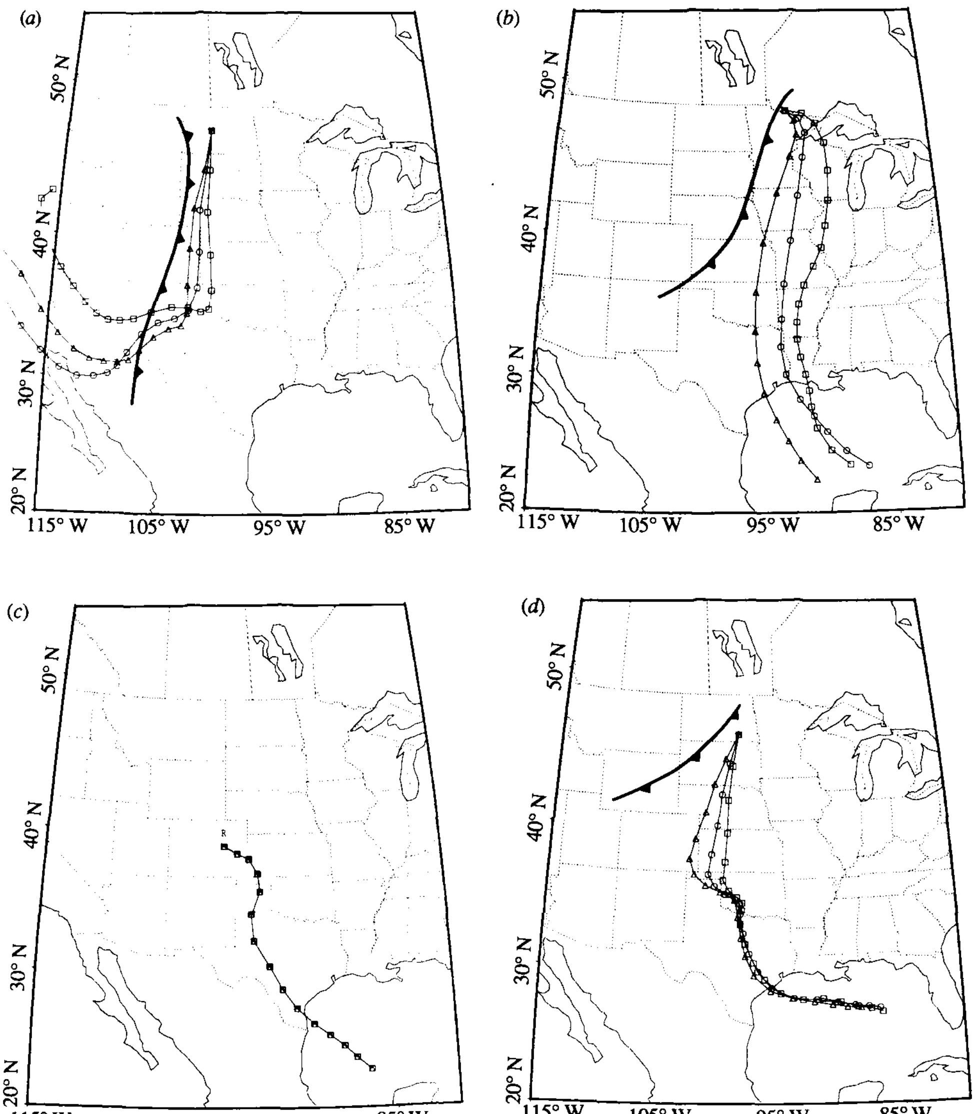

Fig. 2(*a*). Cold front and 6-hourly segments of backward trajectories for three levels terminating at Underwood, N. Dakota on 21 May 1981 at 1800. △, 850 mb; ○, 900 mb; □, 1000 mb; mb, millibar; 1800, 1800 h Greenwich Mean Time (GMT) i.e. 1200 h Central Standard Time (CST). (*b*). Cold front and 6-hourly segments of backward trajectories terminating at Ft. Frances, Ontario on 14 June 1981 at 1800. △, 850 mb; ○, 900 mb; □, 1000 mb. (*c*). Six-hourly segments of backward trajectories terminating at Simla, Colorado on 25 June 1981 at 1800. Rain only was reported in this case. △, 850 mb; ○, 900 mb; □, 1000 mb. (*d*). Cold front and 6-hourly segments of backward trajectories terminating at Berlin, N. Dakota on 27 June 1981 at 1800. △, 850 mb; ○, 900 mb; □, 1000 mb.

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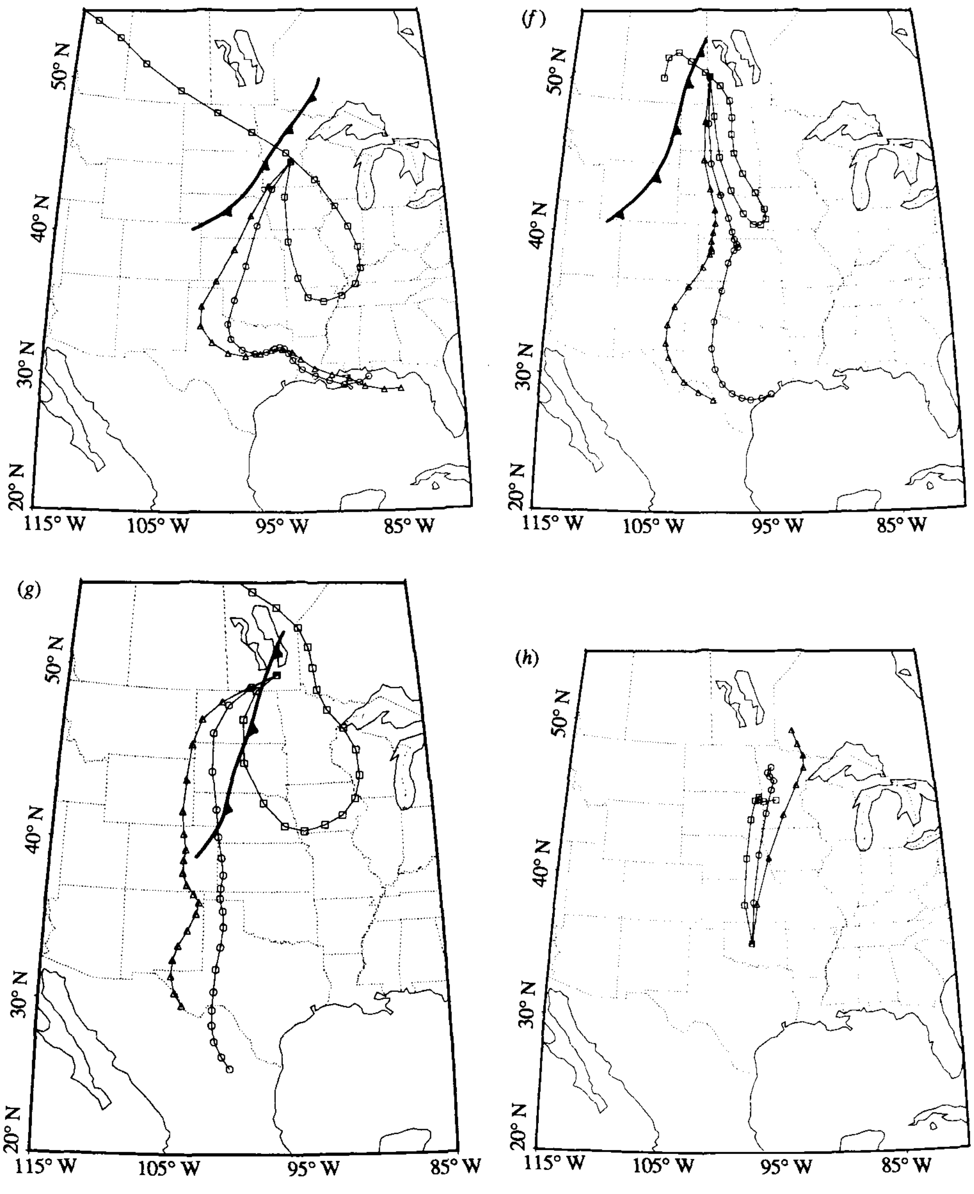

Fig. 2 (*cont.*) (*e*). Cold front and 6-hourly segments of backward trajectories terminating at Buffalo, Minnesota on 28 June 1981 at 1800. △, 850 mb; ○, 900 mb; □, 1000 mb. (*f*). Cold front and 6-hourly segments of backward trajectories terminating at Russell, Manitoba on 1 July 1981 at 1800. △, 850 mb; ○, 900 mb; □, 1000 mb. (*g*). Cold front and 6-hourly segments of backward trajectories terminating at Winnipeg, Manitoba on 2 July 1981 at 1800. △, 850 mb; ○, 900 mb; □, 1000 mb. (*h*). Six-hourly segments of forward trajectories starting from Oklahoma City on 13 June 1981 at 0000 GMT ie. 1800 CST 12 June 1981. △, 850 mb; ○, 900 mb; □, 1000 mb.

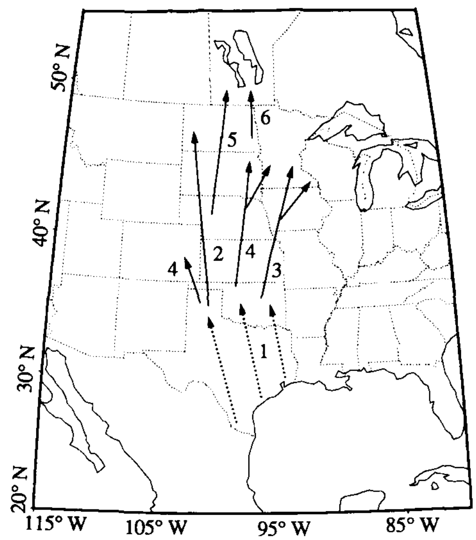

Fig. 3. Development of trajectories in 1981. 1. Suggested trajectories for April and May carrying infected *C. tarsalis*. 2. May 20–21 to Underwood, North Dakota. 3. June 13–14 to Wisconsin and northwestern Ontario. 4. June 25–28 to Colorado, North Dakota and Minnesota. 5. July 1–2 to Manitoba. 6. July 6 onwards to Manitoba.

The interval between the day of arrival and disease in horses was 4–11 days, disease in man 6–11 days, seroconversion in chickens 7–13 days, peak *C. tarsalis* count 1–6 days and virus isolation 4 days. In 12 out of 14 instances the date of arrival coincided with a cold front and rain. In the other two instances there was slight rain on the day of arrival. Minimum temperatures at heights up to 1·5 km were always above 13 °C.

The trajectory to Underwood on 21 May 1981 coincided with the earliest collections of *C. tarsalis* in North Dakota. There were peak collections of *C. tarsalis* in North Dakota at the time of arrival of trajectories at Berlin, North Dakota (North Dakota State Department of Health, 1981).

The sequence of trajectories was from Oklahoma to Wisconsin and Western Ontario on 13 and 14 June, then from 25 to 28 June to Colorado, Minnesota and eastern North Dakota. On 1 and 2 July there were trajectories from Nebraska and South Dakota into Russell and Winnipeg in Manitoba. Subsequent trajectories into Manitoba on 6, 7 and 11 July were from North and South Dakota (Fig. 3).

During July there were further trajectories into Minnesota and North Dakota from Nebraska and further south on 7–8, 10–12, 14 and 30–31 July and into Manitoba from North Dakota and Minnesota on 23, 29 and 30 July.

The trajectories on 13 and 14 June and 27 and 28 June were notable for low level jet winds at 850 mb.

The 120 h trajectory analyses also showed that there were frequent arrivals of trajectories in the Texas Panhandle and Oklahoma from the Gulf Coast of Texas during June and July. Examination of 850 mb Northern Hemisphere charts indicated that such winds also occurred in April and May.

1983. Trajectories were found for the 1983 instances examined (Table 6). The

Table 6. *Source of backward trajectories at 850, 900 and 1000 mb 18, 24 and 30 h previously, together with climatic conditions on arrival for outbreaks of WEE in horses and man, seroconversion in chickens, maximum* C. tarsalis *counts* and virus isolation in 1983*

Location date of diseases etc.	Date of arrival	Source at mb† 850	900	1000	Interval (days)	Conditions
McCreary, Man. 17 June horse	12 June 1983	18 SD (E)	SD (E)	Wis. (C)	5	TFR
		24 Neb. (E)	Neb. (3)	Wis. (S)		
		30 Kan. (N)	Kan. (N)	Iowa (SE)		
Winnipeg, Man. 29 June chicken	20 June 1983	18 SD (SE)	SD (SE)	Wis.	9	TFR
		24 Neb. (E)	Ohio (W)	Wis.		
		30 Kan. (N)	Mis. (N)	Wis.		
Jamestown, ND 7 July horse	2 July 1983	18 Neb. (E)	Iowa (W)	Min.	5	TFR
		24 Neb. (S)	Iowa (W)	Min.		
		30 Kan. (C)	Neb. (E)	Min.		
Winnipeg, Man. 13 July virus 18 July *C. tarsalis*	10 July 1983	18 SD (S)	SD (S)	Min.	3 virus	TFR
		24 Neb. (C)	Neb. (C)	Min.	8 *C. tarsalis*	
		30 Kan. (N)	Kan. (N)	Min.		
	15 July 1983	18 Neb. (C)	Neb. (C)	Iowa	3 *C. tarsalis*	TFR
		24 Kan. (N)	Kan. (N)	Neb. (E)		
		30 Kan. (S)	Kan. (N)	Kan. (N)		

Table 6. (*cont.*)

Dauphin, Man. 22 July chicken	9 July 1983	18 SD (N) 24 SD (E) 30 SD (E)	Min. (W) SD (E) SD (E)	— — —	13	TFR (10 July)
Pelican Rapids, Min. 22 July horse	15 July 1983	18 Kan. (S) 24 Okl. (N) 30 Okl. (S)	Kan. (S) Okl. (N) Okl. (S)	Kan. (NE) Kan. (SE) Okl. (NE)	7	TFR
Bismarck, ND 27 July horse	15 July 1983	18 Kan. (N) 24 Kan. (W) 30 Okl. (W)	Kan. (N) Kan. (W) Okl. (W)	Kan. (N) Kan. (W) Okl. (W)	12	TFR
Marchand, Man. 2 Aug. horse	26 July 1983	18 SD (SE) 24 SD (SE)	SD (SE) SD (SE)	Min. (SE) Min. (SE)	7	TFR
Souris, Man. 10 Aug. horse	2 Aug. 1983	18 ND (W) 24 SD (NW)	ND (S) SD (C)	SD (N) SD (C)	8	TF
Brainerd, Min. 12 Aug. horse	2 Aug. 1983	18 Neb. (E) 24 Kan. (N) 30 Kan. (C)	Iowa (SW) Neb. (SE) Neb. (SE)	Wis. Wis. Wis.	10	TR

*†‡ See footnote to Table 5.

Table 7. *Source of backward trajectories at 850, 900 and 1000 mb 18, 24 and 30 h previously, together with climatic conditions at arrival for outbreaks of WEE in horses and seroconversion in chickens in 1980 and 1982*

Location date of diseases etc.	Date of arrival	Source at mb† 850	900	1000	Interval (days)	Conditions‡
1980						
Rorketon, Man. 27 May horse	23 May 1980	18 SD (S) 24 Neb. (C) 30 Neb. (S)	SD (S) Neb. (C) Kan. (N)	SD (E) Neb. (E) Mis. (NE)	4	T(F)
Benton, Min. 28 May horse	22 May 1980	18 Iowa (C) 24 Iowa (C) 30 Iowa (C)	Iowa (SW) Iowa (S) Iowa (S)	Iowa (SW) Iowa (S) Iowa (S)	6	T
Dauphin, Man. 17 June chicken	11 June 1980	18 SD (N) 24 SD (C)	SD (N) SD (C)	SD (N) SD (C)	6	TFR
1982						
St. Rose du Lac, Man. 6 July horse	2 July 1982	18 SD (C) 24 Neb. (N) 30 Neb. (S)	SD (C) Neb. (N) Neb. (S)	Min. Min. Min.	4	TFR
Portage la Prairie, Man. 26 July horse	15 July 1982	18 SD (NE) 24 SD (SE) 30 Neb. (NE)	SD (NE) SD (SE) Neb. (NE)		11	TFR
Alexandria, Min. 29 July horse	24 July 1982	18 Neb. (C) 24 Kan. (N) 30 Kan. (C)	Neb. (C) Kan. (N) Kan. (C)	Neb. (SE) Kan. (NE) Mis.	5	TFR
Arborg, Man. 18 Aug. horse	12 Aug 1982.	18 Neb. (N) 24 Neb. (C) 30 Neb. (C)	Neb. (NE) Neb. (SE) Wis. (SE)	Min. Min. Min.	6	TFR

† ‡ See footnote to Table 5.

interval between day of arrival and disease in horses was 5–12 days, seroconversion in chickens 9–13 days, peak *C. tarsalis* count 1–8 days and first isolation of virus from *C. tarsalis* 3 days. Eight of the 11 arrivals were associated with a cold front and rain; in one, cold front and rain occurred a day later, and in the other two, rain was present. Temperatures in the trajectories were over 13 °C.

Trajectories were found for peak *C. tarsalis* counts, seroconversion in chickens and disease in horses, events which in themselves did not coincide. During this year there were periods of southerly winds from 11–12 and 19–21 June and from 10 to 20 July, to North Dakota and Western Minnesota.

1980 and 1982. There were few outbreaks in 1980. The trajectories in May in Manitoba and Minnesota were from Nebraska, Kansas and Iowa (Table 7). The arrival in Manitoba may have coincided with a cold front, but there was no coincidence in Minnesota with a cold front or rain. Temperatures during May 1980 were higher than normal.

In 1982 outbreaks in horses were few. Trajectories were from Nebraska and arrival coincided with cold fronts and rain in all four instances (Table 7).

DISCUSSION

Only laboratory-confirmed cases of WEE in horses and man were used to provide dates for the trajectory analysis. During the years examined there was probably under-reporting of cases and insufficient data were available from some areas. Nevertheless the analysis indicates that trajectories from states further south could be correlated with the timing and location of outbreaks of disease in horses or man, seroconversion in chickens, rise in *C. tarsalis* catches and first isolation of WEE virus from *C. tarsalis* in Colorado, Oklahoma, Minnesota, North Dakota, W. Ontario or Manitoba. Thus infected mosquitoes could have been carried on such winds and so introduced WEE virus from further south. Although the dates of the first outbreaks of WEE in July 1981 in South Dakota, Nebraska and Kansas were not available, it is possible that infected mosquitoes could have been carried to these states on the winds shown as terminating in North Dakota and Minnesota on 27 and 28 June 1981.

The distances travelled by the mosquitoes on such winds could have been considerable. For example distances of 1250–1350 km were covered from Oklahoma to Underwood, North Dakota, Blair, Wisconsin and Buffalo, Minnesota in 24, 18 and 24 h respectively, at wind speeds of 50–75 km h^{-1}. It is not known at what time mosquitoes carried on the wind would have arrived. The time of 1800 GMT (1200 CST) was selected for the backward trajectories as the most convenient 6-hourly observation for the time of arrival, while 0000 GMT (1800 CST) was selected for the forward trajectories as being nearest to dusk, when mosquitoes are likely to take off for flight. The forward and backward trajectories led to similar conclusions about arrival of infected mosquitoes (Fig 2*b* and *h*). For the future individual cases could be examined in greater detail, with forward and backward trajectories starting at different times. Thus the possible time of departure and arrival could be determined more precisely.

There was also a correlation in 25 out of 32 instances between arrival and a cold front with rain. In the remaining 7 there was rain in 4 instances and in 2 a possible cold front either nearby or a day later. In the other instance no correlation could be established. Convergence at the cold front would have led to concentration of the mosquitoes.

Given the possibility that infected mosquitoes carried on the wind could have brought WEE virus from further south, the most likely vector is *C. tarsalis*, which is regarded as the primary vector of WEE virus (Brust, 1982*b*; Grimstad, 1983). *C. tarsalis* breeds in temporary sites and has a wide distribution in North America (Mitchell, Francy & Monath, 1980). In the lower Rio Grande valley at Brownsville, Texas *C. tarsalis* is prevalent from October through March with catches in April (Eads, 1965). It was caught in the lower Rio Grande valley and over the border in Mexico in small numbers from June to August 1971 (Sudia *et al.* 1975). *C. tarsalis* was also caught in small numbers in Corpus Christi, Texas – September and October and in Dallas, Texas – August to October (Williams *et al.* 1975; Hopkins *et al.* 1975). On the High Plains of Texas *C. tarsalis* was present from April to October (Harmston *et al.* 1956) with increases occurring in June. In states further north *C. tarsalis* has been caught in Colorado, North Dakota and Manitoba in May, but usually occurs from June to September with peaks in July and August (Mitchell, Francy & Monath, 1980; Brust 1982*b*).

Tempelis (1975) reviewed the host feeding pattern of *C. tarsalis*, which feeds on birds and mammals. In Hale County, Texas, the percentage of *C. tarsalis* feeding on mammals increased in June and July (Hayes *et al.* 1973). In Colorado an increase in mammal feeding was found in May followed by a decrease in June with an increase to a higher level in July, August and September (Tempelis *et al.* 1967). In Kansas and Alberta *C. tarsalis* was found to have fed predominantly on mammals (Edman & Downe, 1964; Shemanchuk, Downe & Burgess, 1963) and in Nebraska cattle and horses, but not chickens, developed antibodies against WEE virus (Hammon, Reeves & Galindo, 1945). The shift in feeding has been found to coincide with WEE in horses and man.

Changes in feeding habits have been considered to be due to the availability of the host, the extent of defensive behaviour by the potential host and host activity patterns (Tempelis, 1975; Day & Edman, 1984).

It can thus be seen that the behaviour of *C. tarsalis* can be used to understand the distribution of WEE and maintenance of the virus. From September to April it is suggested that WEE virus circulates at a low rate in adult *C. tarsalis* and birds along the Gulf Coast of Texas. In spring infected *C. tarsalis* are carried on the wind to northern Texas and Oklahoma, where the cycle continues in birds and to a lesser extent in mammals. In May and early June *C. tarsalis* are carried further north on the warm southerly winds and they may bite birds or mammals giving rise to infection. However further infection may not develop, since the conditions at sites of arrival may not be suitable, in addition the horse is a dead-end host in most cases. In the second half of June and in July more infected *C. tarsalis* are carried north from Oklahoma, Kansas and Nebraska. Depending on their feeding preference, the *C. tarsalis* initiate infection in horses or birds. At the same time they occupy the temporary breeding sites often brought about by the rain at the cold fronts associated with their arrival. Their point of arrival will also be determined by the direction of the warm winds and the meeting of the cold front. Further arrivals of *C. tarsalis* take place and some of the mosquitoes may be infected with WEE virus. Together with local production of *C. tarsalis* such arrivals may maintain the initial infection and lead to an epidemic involving other mosquito species. Later arrivals of *C. tarsalis* may also introduce St. Louis encephalitis virus, which appears later than WEE virus (Monath, 1980). In late August and September, there may be a return migration of *C. tarsalis* that have hatched during the summer further south carrying WEE infection. There would also be non-blood-fed *C. tarsalis* overwintering in the central and northern states.

The migratory pattern of *C. tarsalis* can be seen to be of advantage in using the temporary breeding sites available in the prairie states and provinces and feeding possibly in the past on the bison herds and at present on the mammals.

It has been demonstrated that an amplification cycle takes place in birds, especially house sparrows, before horses and man are involved (Hess & Hayes, 1967). This has been found on the High Plains of Texas involving nestling birds. In Manitoba in 1983, amplification in birds could have taken place as seroconversion in chickens occurred before disease in horses. However, in Manitoba in 1981, disease in horses and man and seroconversion in chickens occurred about the same time, giving no time for amplification. Both in 1981 and 1983 backward trajectories could be correlated with disease in horses and with sero-conversion in chickens. Thus an alternative explanation would be that as far as northern parts of the range are concerned there are introductions of both bird biting and mammal biting *C. tarsalis* and the timing may or may not coincide.

The occurrence of disease earlier in northern areas than in the south (for example in 1981 WEE was earlier in W. Ontario than in Colorado) can be explained by the timing and direction of winds and appearance of cold fronts together with the feeding preferences of the *C. tarsalis* carried on the winds.

Two other species of mosquitoes are involved in transmission, *Cu. inornata* and *Ae. vexans*. The flight activity of *Cu. inornata* is between 9 °C and 18 °C (Meyer, Washino & McKenzie, 1982), thus carriage of WEE virus on the wind by this mosquito would occur earlier in the year and winds with temperature over 20 °C would not be suitable. *Ae. vexans* is known to travel long distances, but the isolation rate of WEE virus from it has been considerably less than that from *C. tarsalis*.

With *C. tarsalis* being involved WEE virus would overwinter in the Gulf Coast. Further north in Manitoba there would be too few *C. tarsalis* overwintering to maintain WEE virus. Transovarial transmission of WEE virus and other alphaviruses in *Aedes* has not been demonstrated (Chamberlain, 1980). WEE virus has been isolated early in the year from April to June in frogs, garter snakes and small mammals and overwintering of virus in these vertebrates may occur. McLintock, Burton & Rempel (1967) found that such isolations were more numerous in non-epidemic than in epidemic years. This may mean that in epidemic years more of these vertebrates become infected, but in the following year factors necessary to initiate an epidemic are not in place. However, there may be other cycles of WEE occurring with *Cu. inornata* and small mammals (Leung *et al.* 1975) (in California a cycle between *Ae. melanimon* and jack-rabbits is described) and in some years virus may enter the *C. tarsalis* bird, horse cycle from the *Cu. inornata* – small mammal cycle.

Table 8. *Possible conditions to be satisfied for epidemic WEE to occur in horses and man in Manitoba, Minnesota and North Dakota.*

Climate	Temperature ⩾ 13 °C up to 1·5 km Warm winds in June and July coming from south (Oklahoma, Texas, Kansas, Nebraska) meeting with cold fronts together with rain. Temperatures maintained during August.
Vectors	Sufficient *C. tarsalis* (i) at source (Texas, Oklahoma, Kansas, Nebraska) (ii) carried on southerly winds (iii) locally* *C. tarsalis* biting horses and man. Other species of local mosquitoes present.
Virus	WEE virus in *C. tarsalis* in source area (Texas, Oklahoma, Kansas, Nebraska) WEE virus in *C. tarsalis* carried on the wind.
Hosts	Susceptible hosts, e.g. birds at source. Susceptible horses and people locally.

* Maximum mean daily count > 50 (Raddatz, 1982, 1986).

Introduction of WEE virus by migratory birds is also possible (Chamberlain, 1980). This would occur in spring, and the virus would have to go through several silent cycles in local mosquitoes before entering the *C. tarsalis* – bird – horse cycle in late June and July.

The timing and location of WEE outbreaks, which may lead to epidemics, can be explained by infected *C. tarsalis* carried on the wind. However, local endemic cycles can still occur.

The 1975 epidemic of WEE virus in the Northern Red River Valley, eastern North Dakota and western Minnesota, and in Manitoba has also been examined (Potter *et al.* 1977; Lillie, Wong & Drysdale, 1976). Historical data for that year were not available on the computer trajectory model.

Examination of 850 mb and surface daily Northern Hemisphere maps for that period showed that southerly winds on 25–26 June 1975 (speed 60–75 km h^{-1} at 850 mb), could have carried *C. tarsalis* mosquitoes infected with WEE virus from Kansas or further south. Such winds met a cold front moving from the west on 26 June 1975, which was followed by heavy rainfall in the Northern Red River Valley over the next few days. An increase in horse cases of WEE in the Northern Red River Valley occurred from 4 July 1975 (Potter *et al.* 1977). Surface southerly winds from 15–17 July 1975 would have carried infected mosquitoes further north into Manitoba meeting a cold front moving from the west on 17 July 1975. An increase of cases of WEE virus in horses in Manitoba occurred from 27 July 1975 onwards (Lillie, Wong & Drysdale, 1976).

WEE virus isolated from 1975 cases in Nebraska, Minnesota and North Dakota (all from *C. tarsalis*) were shown to be indistinguishable by T_1 mapping (Trent & Grant, 1980). They were also indistinguishable from a 1972 isolate from Colorado (source *C. tarsalis*) and a 1973 isolate from Texas (source *Passer domesticus*).

It is interesting to note that in 1987 there was a northward progression of WEE virus cases in horses from Texas (April) through Texas, Oklahoma, New Mexico, Colorado, Kansas (June) to Nebraska, South Dakota, North Dakota and Manitoba in July (Anon, 1987; T. S. Tsai, personal communication, 1987; G. P. S. Nayar, personal communication, 1987).

Factors, which have to be present before an epidemic, are listed in Table 8. These conditions were satisfied in 1981. In 1983, although there were many incursions of warm winds in June and July, the *C. tarsalis* biting mammals did not come in until later in the season. In 1980, there were few mosquitoes. In 1982 there were fronts during late spring and summer, which did not allow southerly winds to come further north, and, in addition, there was probably little or no WEE infection further south. This suggests that there may be a cycle and movement of WEE virus through *C. tarsalis* and vertebrate hosts around the Gulf Coast in Texas and other parts of southern USA and Mexico further west.

Other insects are known to be carried north from Texas, Oklahoma and Kansas (Johnson, 1969; Thresh, 1983). Six-spotted leafhoppers brought aster yellows virus into Manitoba and backward trajectories have been determined (Lee & Robinson, 1958; Westdal, Barrett & Richardson, 1961; Nichiporick, 1965). Leafhoppers and aphids have also been carried on the wind into Wisconsin, Minnesota and North Dakota (Johnson, 1969; Thresh, 1983).

Methods have been developed for predicting epidemics in horses and man in Manitoba (Sekla, 1982). A percentage greater than two of mosquito pools positive for WEE virus, the timing and number of WEE cases in horses greater than six, and seroconversion in chickens have been used (Sekla & Stackiw, 1982; Neufeld & Nayar 1982; Wong & Neufeld, 1982). Raddatz (1982, 1986) developed a biometeorological model based on warmness and wetness which accurately predicts the *C. tarsalis* in Winnipeg 3 weeks later. Between 1980 and 1983, however, there was little correlation between the peak number of *C. tarsalis* in Winnipeg and epidemics in horses and man. Nevertheless, where the *C. tarsalis* females collected per trap per week are 20 or fewer or where the mean daily counts of *C. tarsalis* at Winnipeg do not exceed 50, an epidemic is unlikely (Brust, 1982*b*; Raddatz, 1982). The analysis of WEE outbreaks from 1980–83 indicates that further tests might be possible.

For example, to look for the change from feeding on birds to feeding on large mammals, blood meals from *C. tarsalis* could be analysed for bovine, equine and human blood. Seroconversion in calves, that have lost maternal antibody, could be followed. Rise in temperature, warm southerly winds, rain and cold fronts especially during June and July could be monitored. However, knowledge of the presence of WEE virus, disease and vector in Texas, Oklahoma, Kansas and Nebraska would be important. Once disease has been introduced the use of trajectories to determine source and possible spread could be of advantage.

To protect horses, vaccination before June would be advisable. During the summer it would be preferable to use mosquito repellents on man and horses, rather than spray buildings or breeding sites, as *C. tarsalis* mosquitoes could continue to be introduced on the wind into sprayed areas during the summer.

The results of the analysis have indicated that June and July are the most likely months for wind carriage of infected *C. tarsalis* to occur.

In order to determine in general whether *C. tarsalis* are being carried on the wind, attempts could be made during those months to check take-off at source, the movement downwind at various heights and the landing in association with cold fronts and rain. At the same time chemical. immunochemical and oligonucleotide 'fingerprinting' of *C. tarsalis* and of any WEE strains isolated could be carried out (Trent & Grant, 1980). A technique such as radar, which has been used to detect the flight of spruce budworms (Schaefer, 1976) would probably fail to identify mosquitoes but it may be that insects detectable by radar are being carried in the same airstream as *C. tarsalis* and thus indicate the heights at which to attempt capture.

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