Epidem. Inf. (1987) **98**, 119–125
Printed in Great Britain

Possible windborne spread of myxomatosis to England in 1953

BY R. F. SELLERS*
4 Pewley Way, Guildford, Surrey, GU1 3PY

(*Accepted 30 July 1986*)

SUMMARY

An analysis of the meteorological conditions showed that the first outbreaks of myxomatosis in S.E. England in 1953 could have resulted from wind carriage of insects infected with myxoma virus from northern France. South-easterly winds on the night 11–12 August would have carried the insects 120–160 km from the Départements of Nord, Pas de Calais and Somme across the English Channel to near Edenbridge, Kent. The flight would have taken 6·5–8·5 h at wind speeds of 15–22 km h^{-1}. On the night 11–12 August, temperatures increased with height (inversion) up to 500 m; at ground level temperature was around 19 °C and at 500 m was 25 °C. Insects would have travelled up to the top of the inversion arriving on 12 August as the inversion declined. Two or possibly three generations of infection would have taken place before the disease was seen around the middle of September 1953. The most likely insect was the mosquito *Anopheles atroparvus* which breeds along the coastal marshes of England and northern France and which has been shown experimentally and in the field to transmit myxoma virus mechanically.

INTRODUCTION

The epidemiology of myxomatosis in the Americas, Australia and Europe up to 1965 has been extensively described by Fenner & Ratcliffe (1965). The first case in England was confirmed at Bough Beech, near Edenbridge, Kent (Fig. 1) on 13 October 1953 although the disease probably reached England in August or early September (Ritchie, Hudson & Thompson, 1954; Thompson, 1954). A second case was confirmed at Robertsbridge, East Sussex on 27 October 1953.

In June 1952 Dr P. F. Armand Delille had inoculated two wild rabbits on his estate west of Paris at Maillebois in the Département of Eure et Loir, France, with the Lausanne strain of myxoma virus (Fenner & Ratcliffe, 1965). Later in 1952 the disease was seen in nine départements and, after dying down in the winter months, spread to most départements in France during 1953. By August 1953 it had reached the Départements of Nord, Pas de Calais and Somme which lie along the coast of the English Channel opposite S.E. England (Thompson, 1954).

It is not clear how myxomatosis entered England. It may have been brought by rabbit fleas on birds, through wind carriage of infected insects or by the deliberate introduction of diseased rabbits (Thompson, 1954; Andrewes, 1967). In Australia and France the virus was transmitted mechanically by mosquitoes and

* Present address: Agriculture Canada, Animal Pathology Division, Halldon House, 2255 Carling Avenue, Ottawa, Ontario, KIA OY9.

Table 1. *Insects involved in myxomatosis*

Country	Insect	
Australia	*Culex annulirostris*	(I, F, LT)
	Anopheles annulipes	(I, LT)
	Simuliidae	(I, F)
	Ceratopogonidae	
France	*Aedes caspius*	(I)
	A. detritus	(I)
	Culex modestus	(I)
	Anopheles atroparvus	(I, LE)
	Simuliidae	(LE)
England	*Aedes cantans*	(I)
	A. annulipes	(I)
	Anopheles claviger	(I)
	A. atroparvus	(I, F, LE)

Abbreviations: I, isolation from field caught insects; F, transmission by field caught insects; LT, transmission by laboratory experiments; LE, experimental infection in laboratory.

infected mosquitoes were spread by wind over considerable distances (Fenner & Ratcliffe, 1965; Jacotot, Vallée & Virat, 1958; Joubert *et al.* 1967). In this paper a retrospective analysis has been made of the meteorological conditions, which could have led in 1953 to the introduction on the wind of insects infected with myxoma virus.

GENERAL CONSIDERATIONS

The virus responsible for the outbreak at Bough Beech was shown to be of Grade 1 virulence and indistinguishable from that responsible for the outbreak in France – the Lausanne strain of myxoma virus (Fenner & Marshall, 1957). The mean survival time of rabbits infected with the Lausanne strain was found to be 12·9 days with a range of 10–16 days. Skin lesions were infective from the fifth day after infection until death. Generalized lesions appeared after 6–7 days and the eyes became closed at between days 9 and 11. Field strains of *Anopheles atroparvus* mosquitoes naturally infected with myxoma virus were induced to bite healthy rabbits, and they developed the first signs of myxomatosis on the 7th day and had died on day 13 (Muirhead-Thomson, 1956*b*).

Myxoma virus was isolated in France from *Anopheles atroparvus*, *Aedes caspius*, *Aedes detritus* and *Culex modestus* mosquitoes and in Britain from *Aedes cantans*, *Aedes annulipes*, *Anopheles atroparvus* and *Anopheles claviger* mosquitoes (Service, 1971) (Table 1).

Jacotot *et al.* (1954) showed that *Anopheles atroparvus* was an efficient vector in the laboratory and quoted Roubaud's suggestion that this was a most important vector in France. *Anopheles claviger*, *Anopheles plumbeus* and *Aedes* species were also thought by Roubaud to be involved in transmission.

Andrewes, Muirhead-Thomson & Stevenson (1965) showed that myxoma virus could persist on the mouth parts of infected *Anopheles atroparvus* mosquitoes for 28 days at 60–70 °F (16–21 °C) and for up to 220 days at lower temperatures, although infected mosquitoes might lose up to 20 % of their virus load at each probe

https://doi.org/10.1017/S0950268800061793 Published online by Cambridge University Press

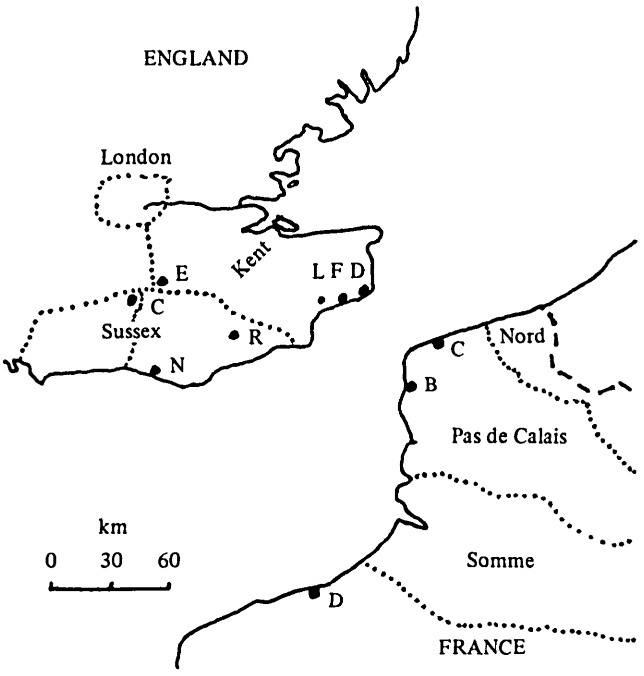

Fig. 1. Location map of northern France and south-eastern England. France: B, Boulogne; C, Calais; D, Dieppe. England: C, Crawley; D, Dover; E, Edenbridge; F, Folkestone; L, Lympne; N, Newhaven; R, Robertsbridge. ---, National boundary ······, Département or county boundary.

(Fenner & Ratcliffe, 1965). Infected mosquitoes could transmit myxoma virus immediately through interrupted feeding or subsequently after 3–7 days when they took another blood meal (Muirhead-Thomson, 1956*b*; Service, 1971). The rabbit flea, *Spilopsyllus cuniculi*, also transmits the virus mechanically (Lockley, 1954) and is considered to be the principal vector in the subsequent spread in England (Mead-Briggs & Vaughan, 1975; Ross, 1982). Virus may remain on fleas for 112 days although some of the infectivity is lost at feeding (Fenner & Ratcliffe, 1965).

HISTORY OF FIRST OUTBREAK

According to Armour & Thompson (1955) the first rabbits with the disease were seen about the middle of September 1953 at Bough Beech. This village lies in the river Eden valley 4·3 km east-north-east of Edenbridge, Kent, 45 km north of Newhaven, East Sussex, and 70 km west by north of the English Channel coast near Lympne, Kent (Fig. 1). Rabbits were sent for examination on 9 October and the diagnosis was confirmed as myxomatosis on 13 October.

Armour & Thompson (1955) have described in detail the subsequent spread around Bough Beech. In addition to the second outbreak at Robertsbridge, East Sussex, a further six outbreaks were confirmed by 5 December 1953 (Thompson, 1954).

Table 2. *Selected meteorological readings at Lympne, Kent, 9 August–1 November, 1953*

Date		Wind Direction (°)	Wind Speed (km h^{-1})	Temperature (°C)
9 Aug.	08.00–15.00	90–130	6–17	14–23
	16.00–18.00	—	0	21–22
	19.00–24.00	90	6–15	16–18
10 Aug.–	13.00–22.00	100–150	2–15	15–22
11 Aug.–	23.00–07.00	80–90	9–17	12–17
	08.00–12.00	100	17–20	18–22
	13.00–21.00	70–90	15–24	19–23
12 Aug.	21.00–08.00	100–120	13–20	19–23
	09.00–16.00	130–160	6–20	25–28
	17.00–24.00	110–150	7–18	22–26
14 Sept.	00.00–12.00	80–110	9–24	11–17
16 Sept.– 17 Sept.	06.00–06.00	130–170	6–22	14–17
10 Oct.– 13 Oct.	12.00–12.00	80–170	7–13	12–16
23 Oct.	00.00–24.00	170–180	7–24	12–14
24 Oct.– 25 Oct.	12.00–06.00	130–170	9–22	12–14
26 Oct.– 27 Oct.	18.00–12.00	150–170	20–33	11–12
31 Oct.– 1 Nov.	06.00–12.00	130–190	15–35	7–12

9–12 August based on hourly observations; remainder based on six-hourly observations.

METEOROLOGICAL CONDITIONS

Table 2 gives details of wind direction, speed and air temperature at Lympne, Kent, during periods when winds blew from the three départéments in northern France towards south-east England. The data are based on the Daily Weather Reports of the Meteorological Office, London (for the whole period) and the hourly observations at Lympne, Kent (8–13 August, 1953). In addition the three-hourly and six-hourly synoptic charts prepared by the Meteorological Office were examined.

Ritchie, Hudson & Thompson (1954) estimated infection occurred in August or early September. Table 2 indicates that periods of suitable winds before 15 September occurred only from 9–12 August and on the morning of 14 September. The 14 September would have been too late for lesions of myxomatosis to have developed by the time they were first observed. During the 9 August calm conditions developed in the late afternoon and the wind speeds would have been too slow (average 10–11 km h^{-1}) to have carried insects the 120–160 km to Bough Beech from northern France. The period 10–12 August was therefore examined in greater detail.

During these days an anticyclone which had been centred on the English Midlands moved across the North Sea north-eastwards to southern Sweden, where it was situated on 12 August.

On two nights windborne carriage of infected insects could have occurred, and that of the 10–11 August was cooler with a minimum temperature of 14 °C. Upper air recordings taken at Crawley, Sussex indicated that on the night of 11–12 August ground temperatures were 19 °C rising to 25 °C at 500 m (temperature inversion). In an inversion, insects tend to be carried on the wind in the stable air at the top of the inversion (Greenbank, Schaefer & Rainey, 1980; Pedgley, 1980). During the first part of the night easterly winds were blowing from the French coast; later the winds veered towards the southeast. With wind speeds of 15–22 km h^{-1} at sea level and 22 km h^{-1} at 500 m, the distance of 120–160 km from northern France to Bough Beech would have been covered in 6·5–8·5 h with the insects flying at a height of up to 500 m. Sunrise and subsequent warming of the land on the 12 August led to the decline of the inversion.

During daytime up-draughts and down-draughts due to convection currents cause turbulence. However, over the sea inversion occurs where the air temperature is higher than sea temperature (Gloster, 1982). During the daytime of 11 August the air temperature over the sea was 19·4 °C and the sea temperature was 17·2 °C (2·2 °C difference), with a wind from the east at speeds of 16–22 km h^{-1}. During the daytime on 12 August the air temperature over the sea was 22·2 °C and the sea temperature was 17·8 °C (4·4 °C difference). South-easterly winds from northern France blew across the Channel with speeds of 6–20 km h^{-1}. Thus there were suitable winds and stable conditions on both days to carry infected insects across the Channel, with the airflow on 12 August being more stable. However, convection currents over land would have broken up the airflow and the insects would not have penetrated far inland.

Thus the most likely period for the wind carriage of infected insects from northern France to Bough Beech would have been the night of 11–12 August. It is possible that the outbreak at Robertsbridge, E. Sussex, which is 15 km from the coast could also have been initiated by infected insects carried across the Channel during these periods.

DISCUSSION

By 11 August, 1953 there was a source of myxoma virus in the Nord, Pas de Calais and Somme départements of northern France (Thompson, 1954) and the wind direction, speed and temperature were such that infected insects could have been carried across the English Channel and several kilometres inland to Bough Beech, Edenbridge, during the night of 11–12 August, 1953. The period from the 12 August, 1953 until the middle of September, 1953 when the disease was first seen – 34 days – means that a number of generations of infection must have occurred. The results obtained by Myers (1954) in trial releases in Australia indicate that the first deaths would occur 9–16 days after release. If the insects did not bite the rabbits until 4–7 days after arrival (Muirhead-Thomson, 1956*b*; Service, 1971) there would be an interval of 13–16 days before deaths occurred. Thus it is possible that the numbers of affected rabbits were sufficient only at the second or third generation for the disease to be noted, i.e. in mid-September. By the time of confirmation in October, 1953, 200 acres (80 ha) had diseased rabbits (Armour & Thompson, 1955), a spread of about 6 acres (2·4 ha) a day since 12 August.

Given the possibility of windborne carriage of infected insects across the Channel, it is still uncertain which species could have carried myxoma virus. In Australia mosquitoes (*Culex annulirostris* and *Anopheles annulipes*), Simuliidae and Ceratopogonidae have been implicated in carrying the virus over long distances (Fenner & Ratcliffe, 1965). In France mosquitoes (*Anopheles atroparvus*, *Aedes caspius* and *Aedes detritus*) and Simuliidae were suspected (Jacotot *et al.* 1954; Joubert *et al.* 1967; Joubert & Monnet, 1975) (Table 1).

Anopheles atroparvus is found in both France and England. It breeds in coastal marshes, especially low-lying areas are along the south and east coasts and it also breeds on the coastal marshes of northern France, Belgium and Holland. It was considered to be the main vector of malaria in Northern Europe (Jacotot *et al.* 1954).

Anopheles atroparvus feeds on mammals. In England it was taken in 1954 biting rabbits in a built-up area in Newhaven, E. Sussex, indicating that flight had occurred away from its normal habitat (Muirhead-Thomson, 1956*b*). It takes blood meals at intervals during the cold weather from November until April. Thus, in addition to the rabbit flea, it could carry over myxoma infection from one year to the next in those areas where it is found. The other mosquitoes implicated in the spread of myxomatosis in England are woodland species of *Aedes* (Muirhead-Thomson, 1956*a*), which would not be expected to disperse far from their habitat. Salt marsh mosquitoes, for example *Aedes sollicitans*, are well known for being carried long distances (up to 175 km) on the wind (Johnson, 1969).

Thus, *Anopheles atroparvus* would appear to be the most likely mosquito to have carried myxoma infection from northern France. However, it is not possible to exclude Simuliidae and Ceratopogonidae.

The meteorological conditions were similar to those found for the carriage of insects infected with viruses that are biologically transmitted (Pedgley, 1983; Sellers, 1983). The aphid plant virus vector, *Myzus persicae*, was shown to be carried across the Channel from the Continent to England by easterly and south-easterly winds in July, 1947 (Hurst, 1969). Similar meteorological conditions were found, apart from temperature, for transport of foot-and-mouth-disease virus across the Channel (Gloster, 1982; Gloster, Sellers & Donaldson, 1982; Donaldson *et al.* 1982). Thus it would appear that when animals or plants in northern France are affected by infectious organisms, there is always the chance that suitable winds may transport the organism or its vector across the Channel to England.

There were further periods of south-easterly winds after the middle of September (Table 2), but it is difficult to say whether there were further incursions of insects infected with myxoma virus across the Channel. Once myxomatosis was known to be present in England, inhibitions on spreading the disease by deliberate release of infected rabbits would have diminished. Nevertheless dispersion over distance by infected *Anopheles atroparvus* may also have occurred during the subsequent epidemic as suggested by Service (1971).

It is a pleasure to acknowledge the counsel and help of John Gloster, Meteorological Office, Bracknell, especially in his explanation of the relevant meteorological data. Thanks are also due to John Ross, Agricultural Science Section, MAFF, Worplesdon for information and comments. The permission of the Meteorological Office for the use of the data is gratefully acknowledged.

REFERENCES

ANDREWES, C. H. (1967). Evolution in action: myxomatosis. In *The Natural History of Viruses*, pp. 149–161. London: Weidenfeld & Nicolson.

ANDREWES, C. H., MUIRHEAD-THOMSON, R. C. & STEVENSON, J. P. (1965). Laboratory studies on *Anopheles atroparvus* in relation to myxomatosis. *Journal of Hygiene* **54**, 478–486.

ARMOUR, C. J. & THOMPSON, H. V. (1955). Spread of myxomatosis in the first outbreak in Great Britain. *Annals of Applied Biology* **43**, 511–518.

DONALDSON, A. I., GLOSTER, J., HARVEY, L. D. J. & DEANS, D. H. (1982). Use of prediction models to forecast and analyse air borne spread during the foot-and-mouth-disease outbreaks in Brittany, Jersey and the Isle of Wight in 1981. *Veterinary Record* **110**, 53–57.

FENNER, F. & MARSHALL, I. D. (1957). A comparison of the virulence for European rabbits (*Oryctolagus cuniculus*) of strains of myxoma virus recovered in the field in Australia, Europe and America. *Journal of Hygiene* **55**, 149–191.

FENNER, F. & RATCLIFFE, F. N. (1965). *Myxomatosis*. Cambridge: University Press.

GLOSTER, J. (1982). Risk of airborne spread of foot-and-mouth disease from the Continent to England. *Veterinary Record* **111**, 290–295.

GLOSTER, J., SELLERS, R. F. & DONALDSON, A. I. (1982). Long distance transport of foot-and-mouth-disease virus over the sea. *Veterinary Record* **110**, 47–52.

GREENBANK, D. O., SCHAEFER, G. W. & RAINEY, R. C. (1980). Spruce budworm (Lepidoptera: Tortricidae) moth flight and dispersal: new understanding from canopy observation, radar and aircraft. *Memoirs of the Entomological Society of Canada*, No. 110.

HURST, G. W. (1969). Meteorological aspects of insect migrations. *Endeavour* **28**, 77–81.

JACOTOT, H., TOUMANOFF, C., VALLÉE, A. & VIRAT, B. (1954). Transmission expérimentale de la myxomatose au lapin par *Anopheles maculipennis atroparvus* et *Anopheles stephensi*. *Annales de l'Institut Pasteur* **87**, 477–485.

JACOTOT, H., VALLÉE, A. & VIRAT, B. (1958). Etude expérimentale de la myxomatose. *Bulletin de l'Académie Vétérinaire de France* **31**, 269–278.

JOHNSON, C. G. (1969). Migration and Dispersal of Insects by Flight. London: Methuen.

JOUBERT, L. & MONNET, P. (1975). Vérification expérimentale du rôle des *Simulies* (*Tetisimulium bezzii* Corti 1914 et *Odegmia* group ornatum) dans la transmission du virus myxomateux en Haute Provence. *Revue de Médicine Vétérinaire* **126**, 617–634.

JOUBERT, L., OUDAR, J., MOUCHET, J. & HANNOUN, C. (1967). Transmission de la myxomatose par les moustiques en Carmargue. Rôle preéminent de *Aedes caspius* et des *Anopheles* du groupe *maculipennis*. *Bulletin de l'Académie Vétérinaire de France* **40**, 315–322.

LOCKLEY, R. M. (1954). The European rabbit flea, *Spilopsyllus cuniculi* as a vector of myxomatosis in Britain. *Veterinary Record* **66**, 434–435.

MEAD-BRIGGS, A. R. & VAUGHAN, J. A. (1975). The differential transmissibility of myxoma virus strains of differing virulence grades by the rabbit flea *Spilopsyllus cuniculi* (Dale). *Journal of Hygiene* **75**, 237–247.

MUIRHEAD-THOMSON, R. C. (1956*a*). The part played by woodland mosquitoes of the genus *Aedes* in the transmission of myxomatosis in England. *Journal of Hygiene* **54**, 461–471.

MUIRHEAD-THOMSON, R. C. (1956*b*). Field studies on the role of *Anopheles atroparvus* in the transmission of myxomatosis in England. *Journal of Hygiene* **54**, 472–477.

MYERS, K. (1954). Studies in the epidemiology of infectious myxomatosis of rabbits. II. Field experiments, August–November 1950 and the first epizootic of myxomatosis in the riverine plain of south-eastern Australia. *Journal of Hygiene* **52**, 47–59.

PEDGLEY, D. E. (1980). Weather and airborne organisms. Technical Note 173. World Meteorological Organisation, Geneva.

PEDGLEY, D. E. (1983). Windborne spread of insect-transmitted diseases of animals and man. *Philosophical Transactions of the Royal Society of London* B **302**, 463–470.

RITCHIE, J. N., HUDSON, J. R. & THOMPSON, H. V. (1954). Myxomatosis. *Veterinary Record* **66**, 796–804.

ROSS, J. (1982). Myxomatosis: a natural evolution of the disease. *Symposium of the Zoological Society of London* **50**, 77–95.

SELLERS, R. F. (1983). Seasonal variations in the spread of arthropod-borne disease agents of man and animals: implications for control *Philosophical Transactions of the Royal Society of London* B **302**, 485–495.

SERVICE, M. W. (1971). A reappraisal of the role of mosquitoes in the transmission of myxomatosis in Britain. *Journal of Hygiene* **69**, 105–111.

THOMPSON, H. V. (1954). The rabbit disease: myxomatosis. *Annals of Applied Biology* **41**, 358–366.