# Re-assessing the likelihood of airborne spread of foot-and-mouth disease at the start of the 1967–1968 UK foot-and-mouth disease epidemic

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#### SUMMARY

The likelihood of airborne spread of foot-and-mouth disease at the start of the 1967–1968 epidemic is re-assessed in the light of current understanding of airborne disease spread. The findings strongly confirm those made at the time that airborne virus was the most likely cause of the rapid early development of the disease out to 60 km from the source. This conclusion is reached following a detailed epidemiological, meteorological and modelling study using original records and current modelling techniques. The role played by 'lee waves' as the mechanism for the spread is investigated. It is thought that they played little part in influencing the development of the epidemic. A number of lessons learned from the work are drawn, identifying the need for further research on the quantity and characteristics of airborne virus. The results are also used to illustrate what advice would have been available to disease controllers if the outbreak had occurred in 2004.

#### INTRODUCTION

The 2001 UK epidemic of foot-and-mouth disease (FMD) is a clear reminder of the economic significance of the disease and the importance of rapid diagnosis and control once disease is present. It has been estimated that that losses to agriculture and the food chain were £3·1 billion [1]. In addition some £2·5 billion was paid by the UK Government in compensation for slaughtered animals and clean-up costs. Losses of between £2·7 and £3·2 billion were also experienced in tourism and businesses directly affected by tourism [2, 3]. To ensure that future outbreaks are managed effectively, it is essential to have a

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detailed understanding of the disease and how it spreads. Whilst every outbreak will display its own unique characteristics there is considerable merit in examining past outbreaks in order to learn important general lessons for the future.

In 1967–1968 the United Kingdom experienced a large FMD epidemic. It commenced in October 1967 and finished in June 1968. By the time it finished a total of 2364 outbreaks were recorded (2228 in the Northwest Midlands and North Wales, 52 in Derbyshire, 49 in the Southwest Midlands and South Wales, 22 in Lancashire and Westmorland and 13 in the East Midlands). A total of 433 987 animals were slaughtered [4].

The Report of the Committee of Inquiry [4] investigated the possibility that FMD might have been transmitted on the wind, an idea hypothesized in the early 1900s by a number of workers including

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Penberthy [5] and Bang [6, 7]. The Report brought to the forefront the requirements for detailed meteorological, epidemiological and laboratory studies. Hugh-Jones & Wright [8] investigated the relationship between disease spread, wind and precipitation. They concluded that the evidence strongly supported the hypothesis that the weather played a major part in disease spread. Tinline [9] suggested that initial spread could have been caused by the presence of special atmospheric conditions which produced mountain or lee waves to the east of the Welsh Mountains. The formation of lee waves is discussed later.

The course of the epidemic and the epidemiology are recorded in the Reports of the Animal Health Services of the Ministry of Agriculture, Fisheries and Food (MAFF) in Great Britain [10, 11].

On 17 and 18 October 1967 two gilts from Bryn Farm, Oswestry, Shropshire were turned out with a boar for service. They were out for most of the day in the yard and in the adjacent field. On Saturday, 21 October 1967 the owner noticed that one gilt was lame; one day later a second gilt was seen to be lame. Both animals were removed from the yard and housed. By 25 October a third sow and 11 store pigs were ailing and at this stage veterinary advice was sought. The inspector diagnosed FMD at 15:40 hours GMT. By the morning of 26 October 28 pigs were infected out of a total of 67 on the farm. At the diagnostic inquiry on 26 October, the oldest lesions were found in the two gilts and were estimated at 4 days old, recent lesions were found on other pigs on the premises. None of the 71 cattle or 47 sheep also on the farm showed any clinical signs of the disease. The entire stock was slaughtered on that day.

Whilst it was not possible to establish conclusively the initial cause of the introduction of infection, there was sufficient circumstantial evidence to suggest that infected Argentine lamb bones fed to the owner's dogs were also eaten by the two sows when they were in the field or in the farm yard on 17 and 18 October.

The period under investigation, up to and including 5 November 1967, falls into three phases – the primary outbreak at Bryn Farm in pigs (phase 1), outbreaks within 5 km of Bryn Farm, 28 October to 1 November (phase 2a), outbreaks 16–54 km north-east of Bryn Farm, 30 October to 1 November (phase 2b) and outbreaks around Bryn Farm and up to 60 km north-east of Bryn Farm (phase 3). The choice of dates for the second and third phases is based on the investigations of Wright [12] and Hugh-Jones &

Wright [8]. Details of the outbreaks in each of the three phases are given at Table 1. Up to 1 November 1967 there were 20 secondary outbreaks around Bryn Farm, of which one was attributed to spread by a person and two to vehicles collecting milk churns. Up to 1 November 1967 there were 16 outbreaks to the north-east of Oswestry. Four of these were considered by MAFF to be primaries associated with imports of Argentine lamb through feeding of bones to dogs or handling of meat and cattle. The fifth primary outbreak was reported on 3 November 1967; on that farm there was handling of meat and cattle by a person. No outbreaks due to controllable methods of spread other than meat, persons or churn collections were recorded for the period 25 October to 5 November.

Subsequent to these studies in the early 1970s much progress has been made with understanding the disease and the role that airborne virus plays in disease spread. A full review concerning the pathogenesis, spread and diagnosis of FMD is given by Alexandersen and others [13]. In summary, it has been established that infected animals excrete virus into the atmosphere. Pigs emit significantly more virus than either cattle or sheep [13-19]. Once airborne, virus particles are subject to environmental factors that influence their rate of biological and physical decay. Biological decay has been shown to be influenced by relative humidity (RH). Investigations have shown that above 60% RH the virus survives for extended periods and that below this level it rapidly becomes inactivated [20]. The concentration of airborne particles at a given location is dependent on additional factors, including atmospheric conditions prevalent at the time and the topography. Highest concentrations can be expected typically in stable conditions with low wind speeds which result in low levels of turbulence and hence minimal mixing. In contrast high wind speeds or a convective atmosphere will result in rapid mixing and much lower downwind concentrations.

The minimum dose to infect cattle and sheep has been established for some FMD strains, and both species are highly susceptible to infection by the airborne route being infected by as little as 10 infectious units when exposed for 5–10 min, while pigs require a much larger dose by this route (>800). Here, 1 infectious unit is defined as the amount of virus that will infect 50% of a highly susceptible cell culture, i.e. tissue culture infectious dose 50% (TCID<sub>50</sub>). Based on these short-term experiments the assumption is

Table 1. Epidemiological details

Phase	Location	No. of outbreaks	Date of confirmation	Date of earliest lesions	Outbreaks and species affected	Source of infection*
1	Bryn Farm	1	25 Oct.	21 Oct.	1P	Lamb bones†
2a	Farms within 5 km of Bryn Farm‡	20‡	28 Oct. to 1 Nov.	27 Oct. to 1 Nov.	12C, 3CS, 4S, 1?	1 farm worker, 2 milk churn collection, 17 local/unknown
2b	16–52 km north-east of Bryn Farm	16	30 Oct. to 1 Nov.	29 Oct. to 1 Nov.	16C	4 lamb meat and bones, 12 unknown
3	Farms around Bryn Farm and 10 km and more to north-east	58	2 Nov. to 5 Nov.	?	2P, 1PC, 2CS, remainder majority C with some S	1 lamb meat, 2 milk churn collection, 55 local/unknown

C, cattle; CS, cattle and sheep; S, sheep; P, pigs; PC, pigs and cattle; ?, unknown.

that for extended exposure, say over 24 h, a minimum concentration of 0.06-0.07 TCID<sub>50</sub> m<sup>-3</sup> is needed to infect cattle, the most susceptible species by this route, 0.6-0.7 TCID<sub>50</sub> m<sup>-3</sup> to infect sheep and at least 16 TCID<sub>50</sub> m<sup>-3</sup> to infect pigs [13, 18, 19, 21–24]. It should, however, be emphasized that this is an assumption based entirely on short-term experiments. In comparison, pigs require  $10^4-10^5$  TCID<sub>50</sub> and cattle  $10^5-10^6$  TCID<sub>50</sub> by the oral route to become infected [13].

Over the years a number of detailed atmospheric models have been developed to help predict areas at risk from airborne FMD virus. These include the UK Met Office's atmospheric dispersion model (NAME) and Cambridge Environmental Research Consultants, UK short-range atmospheric dispersion model (ADMS), the Local Scale Model Chain (LSMC) including the Rimpuff dispersion model and the Danish Emergency Response Model of the Atmosphere (DERMA) [25–32]. All of these models were actively used in the 2001 UK FMD epidemic, but to date none have been used on the start of the 1967–1968 UK epidemic [33–35].

Experience of modelling past outbreaks has shown that atmospheric dispersion models can generally predict the basic pattern of disease spread. However, shortly after the epidemic Tinline [9] suggested that the presence of lee waves may have influenced the pattern of disease spread. Lee or mountain waves are formed when air is forced to rise over a hill or mountain rather than passing around it. If this occurs simultaneously with the presence of a stable atmospheric layer above the mountain, vertical movement of the air is restricted. As the air is forced over the mountain its wind speed increases, cools and condenses, forming a mountain wave cloud over the summit. Once over the mountain the air descends and warms. A wave-like pattern then becomes established downwind of the mountain range, with the air 'bouncing' between the surface and the stable layer above. The air can become very turbulent with both updraughts and downdraughts and these waves can extend for many kilometres downwind. Where the air rises condensation can take place and roll clouds or lenticular clouds form. Associated with the downdraughts, surface winds are occasionally present in the opposite direction to the main synoptic winds. Tinline [9, 36] proposed that the down currents could have brought virus particles to the surface many kilometres downwind, causing a number of secondary

<sup>\*</sup> The sources of infection are those given at the time by MAFF.

<sup>†</sup> Originally 40 farms were considered to have been infected by meat from South America. Lamb meat or bones from Argentine Establishment 1408 had been supplied to 24 of the 40 farms. The 24 farms included Bryn Farm and the other five in the table. The four farms confirmed on 30 and 31 October were 16, 21, 22 and 48 km north-east of Bryn Farm. The farm confirmed on 3 November was 10 km north-east of Bryn Farm.

<sup>‡</sup> Of the 20 farms within 5 km of Bryn Farm 12 were in the sector north to east, 5 east to south, 2 south to west and 1 west to north of Bryn Farm. The farm on which the source was attributed to a farm worker and one of the two farms on which the source was attributed to milk churn csollection were north to east of Bryn Farm. The other one of the two farms was east to south of Bryn Farm.

infections. To explore this possibility two questions require answers. First, were lee waves present at the time virus was released and secondly, would the atmosphere have been so turbulent that virus would have been evenly distributed throughout the boundary layer reducing the ground level concentration at a particular location and, therefore, reducing the likelihood of infection. The basic conditions for lee-wave formation are:

- A wind speed of at least 15 knots (kt) blowing nearly at right angles to the ridge (within 30°).
  Knots are the internationally used unit for reporting wind speed (1 kt is 0.51 m/s).
- An inversion or stable layer not far from the ridge top with a deep layer of less stable air above it.
- An increase in wind strength with height, but the direction remaining fairly constant.

This paper re-investigates the start of the 1967–1968 FMD epidemic in the light of our current understanding of how airborne spread of FMD virus takes place. Particular emphasis is given to modelling the airborne disease spread and exploring the lee-wave hypothesis. The overall purpose of the work being to develop a clearer understanding of the aerobiological factors which determine the airborne spread of FMD and identify the lessons learnt for those responsible for controlling and eradicating future disease outbreaks.

# MATERIAL AND METHODS

#### **Infected premises**

The locations of the 95 farms involved in the first few weeks of the epidemic and the sequence of events were obtained from a number of sources. First, from detailed manuscript records held by one of the authors (R.F.S.) and others stored at the Institute for Animal Health, Pirbright. One of these was a copy of an original manuscript written by the Veterinary Officer responsible for disease reporting in the Oswestry area. Second, from the literature [4, 8, 9, 12, 36]. Third, from a discussion with the original owner of Bryn Farm, the first reported outbreak in the epidemic.

All of this information together with similar data from a number of other FMD outbreaks is now being collated at the Institute for Animal Health, by the authors as part of a Department of the Environment, Food and Rural Affairs (Defra) contract. This will permit the outbreaks to be re-analysed in the light of increased knowledge concerning disease spread.

## Virus emission

The virus emission pattern from an infected premise is estimated using a Virus Production Model [37]. The numbers and type of animals with vesicular lesions at confirmation/slaughter are combined with the results of laboratory experiments, using the same/similar virus strain, to determine a total 24-h virus release (TCID<sub>50</sub> log units per 24 h). This calculation is repeated for each day that virus was excreted into the atmosphere.

The scenario applicable to Bryn Farm was estimated from the reported sequence of events together with results from experimental work carried out after the epidemic to determine the total 24-h release from pigs infected with O1 BFS1860 virus. This strain was isolated from epithelium collected on 1 November 1967 from infected cattle on a farm near Wrexham [14, 38]. BFS1860 virus was found to be excreted from pigs at peak levels of between 5-9 and 6-4 logs TCID<sub>50</sub> per 24 h. A peak level of 6-2 logs TCID<sub>50</sub> per 24 h has been used for the daily calculation.

It has been assumed that the first two pigs became infected simultaneously and exhibited 'day 0' lesions on 21 October. This was followed on 23 October by a second generation of 12 pigs and a further 14 on 24 October. Whilst this assessment is speculative it is consistent with that reported at the time of slaughter.

# Secondary infection periods

For each farm included in this study where secondary disease spread occurred, an infection window, based on the work by Hugh-Jones & Wright [8] and Sellers & Foreman [39], was established. It has been assumed that for between-farm airborne spread, a period of 4–14 days is possible. In this paper an infection window of 3–17 days has been used to allow for an accuracy of  $\pm 1$  day in dating lesions between 0 and 5 days old and a decrease in accuracy thereafter [35, 40].

# Meteorological data

Synoptic weather charts were obtained from the National Meteorological Archive (NMA), based at Bracknell. These were used to determine the general

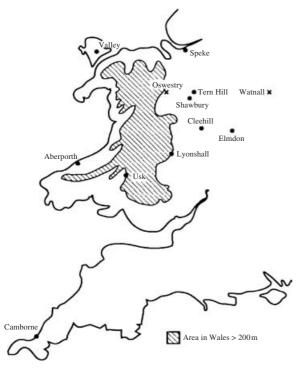


Fig. 1. Location of meteorological observing stations used in this study together with the area of ground in Wales with a height of > 200 m.

characteristics of the atmosphere at the time of virus release.

Surface meteorological data were extracted from original manuscript records, held at the NMA, for a number of weather-observing stations (Shawbury, Tern Hill, Lyonshall, Clee Hill, Valley, Speke, Elmdon and Watnall). The stations were selected in order to determine the likely status of the atmosphere near the initial disease foci, in the Cheshire Plain where many of the secondary outbreaks were recorded and further to the east. The location of all of the meteorological observing stations used in this study together with the area of ground in Wales with a height of >200 m are given at Figure 1.

Hourly observations from the Met Office observing station at Shawbury were used as one of the prime data sources. This information had been used by Hugh-Jones & Wright [8] and was the closest to the initial disease foci. The observations included wind speed and direction, RH, cloud amounts, heights and types, present and past weather, precipitation and temperature.

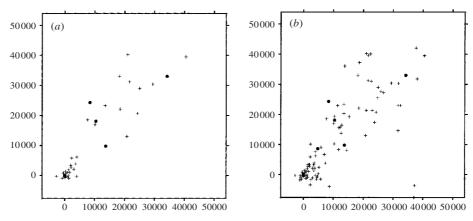
All of the stations studied above are at low level and hence may not truly represent conditions on the higher ground of the exposed Welsh Mountains. To explore this aspect the Shawbury 10-m observations were compared with the geostrophic wind directions extracted from the synoptic weather charts. The geostrophic wind represents the flow of air in frictionless conditions (above 500–1000 m). The geostrophic wind flows parallel to the isobars [41].

This vertical profile of temperature and wind was obtained from radiosonde ascents from Aberporth on the Welsh coast. Radiosondes were released at 0600 hours each day between 23 and 26 October with no data being available for 21 or 22 October, as this was a weekend.

Weather forecasters develop their own expertise in predicting the occurrence of lee waves. The proximity of the Met Office at Shawbury to the Welsh Mountains combined with its responsibility for forecasting the weather for trainee pilots makes it ideally situated for assessing the potential for lee waves in the vicinity of the FMD epidemic. The only readily available guide to the forecaster is the 'Caswell method' of prediction [42]. Caswell's method involves calculating a parameter, which is a function of the stability, wind speed and vertical wind shear of the atmosphere. Values for the parameter are obtained for two layers (1000–700 mb and 700–300 mb) and the existence or not of lee waves are determined from a graph. Where waves are predicted, Caswell's method gives information on the likely wavelength and the maximum vertical velocity of the air's motion. Experience has shown that this method should be used with caution as it treats the troposphere in two smoothed layers, over its entire depth. In practice a forecaster examines the synoptic situation, the weather observations from a range of locations and the 3D structure of the atmosphere, and then makes an assessment of the potential for lee waves. The 'Caswell method' is then used to support or contradict this assessment. This joint approach has been used in this paper.

#### Atmospheric dispersion modelling

The ADMS short-range dispersion model [28] was used to determine the hourly downwind virus concentration from Bryn Farm. Given the distances involved in this epidemic it would have been preferable to use a full 3D dispersion model such as the Met Office operational dispersion model (NAME). However NAME requires derived gridded meteorological data which were not readily available for 1967. Under neutral and unstable atmospheric conditions NAME and ADMS have been compared very favourably [43].



**Fig. 2.** Location of infected premises included in this study. (a) Shows the farms affected between 25 October to 1 November; (b) shows the farms affected between 25 October and 5 November. Bryn Farm is located at 0, 0 as a solid square. Farms which received meat from the same consignment as Bryn Farm are shown as solid circles. All of the remaining farms are denoted by +. The figures are orientated north to south with scales in metres.

A daily virus emission, together with hourly values of wind speed and direction, cloud amount, surface air temperature, latitude, time of year and day were input in to the model. It was assumed that the daily emission value was emitted at a steady rate throughout each day/night and that Shawbury observations were representative of the conditions experienced at Bryn Farm. With the wide distribution of secondary outbreaks an area of approximately  $60 \times 60$  km was selected for modelling. Maximum hourly virus concentrations, in  $TCID_{50}$  m<sup>-3</sup>, at approximately 3000 grid points evenly distributed throughout this area were calculated for each hour and for the full period 21-26 October.

The topography routine within ADMS was not used primarily because of the very complex nature of the topography in the immediate vicinity of the source farm. A topographical dataset, with a horizontal resolution of  $\sim 100$  m or less would have been required to capture the intricate nature of the topography and this was not available. In addition it would have been extremely difficult to represent the local topography as a function of the Welsh Mountains to the west. Consequently only a simple qualitative estimate for topography has been used in this study.

#### **RESULTS**

# **Epidemiology**

Figure 2(a, b) gives the locations of all 95 farms included in this study. Figure 2a shows the farms affected between 25 October and 1 November corresponding to phases 1, 2a and 2b and Figure 2b the

farms affected between 25 October and 5 November corresponding to phases 1, 2a, 2b and 3. It can be seen that there is a cluster of infected premises within 5 km of Bryn Farm (grid location 0, 0) and with a few isolated exceptions, the remainder located to the north-east in a sector  $20^{\circ}-60^{\circ}$ . Figure 2aalso identifies the four other farms which received meat from the same consignment as Bryn Farm and Figure 2b the remaining farm receiving meat from the same consignment. There would appear to be no definite grouping of premises in the north-east sector up to and including 1 November. The furthest farm which has been included in this study is  $\sim 60 \text{ km}$ from Bryn Farm. Hugh-Jones & Wright [8] identified around 13 outbreaks which were at least 60 km, but the majority were reported during the middle to end of November and fall outside the scope of this paper.

The estimated virus emission pattern from the infected pigs at Bryn Farm is given at Table 2. If this scenario represents the unfolding disease sequence it suggests that virus release was at a peak on 25 October, but with significant amounts from 22 to 26 October.

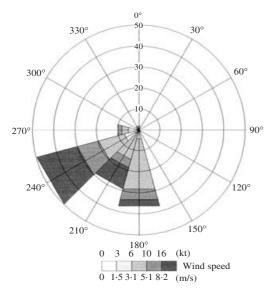
All of the premises included in this study fell well within the 3–17 days infection period identified as being possible for infection from virus emitted from Bryn Farm. FMD was confirmed at each of the farms by 5 November.

## Meteorology

On 21 October the winds were light and variable and there were 8 h when calm winds were recorded at

Table 2. Estimated atmospheric virus emission pattern for Bryn Farm (TCID<sub>50</sub> log units per 24-h period)

21 Oct.	22 Oct.	23 Oct.	24 Oct.	25 Oct.	26 Oct.
2.2	6.5	6.5	7.2	7.6	7.3



**Fig. 3.** Shawbury wind rose for the period 21–26 October 1967. The number of hours when the wind was blowing from a given direction is plotted as a function of wind speed (kt and m/s).

Shawbury. For the period 22–26 October there was a moist south to north-westerly airflow over the United Kingdom and particularly in the vicinity of the infected area. Overall the days and nights were cloudy, mild and moist. The RH was above 60% for the whole period and rain and drizzle was recorded on 4 days at Shawbury. These conditions would have favoured virus survival. The wind strength generally increased with time, being particularly strong on 26 October; hourly wind speeds were around 20 kt and a maximum gust of 40 kt was recorded at Shawbury. Using data from Shawbury a wind rose for the period 21–26 October is given in Figure 3. The figure shows the number of hours in the period when wind was blowing from a particular direction, together with information about the wind speed. The wind speed at Bryn Farm exposed to the south and south-west may have been even stronger (see Discussion).

The results of all the lee-wave analyses are recorded in Table 3. In summary it is likely that lee waves were present on 23 (morning only), 24 (late morning and afternoon) and 25 October (morning), but not on the other days. The lack of upper air data for the first 2 days means that only a subjective assessment as to the likelihood of waves could be made based upon the surface observations.

## Modelling

The maximum hourly virus concentrations in TCID<sub>50</sub> m<sup>-3</sup>, for the period 21–26 October, based on Shawbury observations are given in Figure 4. There are two distinctive areas of higher concentrations, one to the north and one to the north-east. Apart from farms very close to the source there are no infected farms within the plume to the north but the majority of secondary farms are co-incident with the plume to the north-east.

## Detailed analysis for each day of virus release

#### 21 October

The midnight synoptic chart shows a predominantly south-westerly airflow affecting Wales and the West Midlands, although weak ridging to the south lead to a lighter and more variable flow over southern parts of Shropshire.

The observations as recorded in Shawbury's daily register show the surface being calm until after 0700 hours when light south-westerlies set in before veering westerly towards the end of the morning, becoming calm or a very light north to north-westerly during the afternoon.

In view of the calm to light winds it is hard to quantify the 'footprint track' of virus released from Bryn Farm. Any virus released into the atmosphere would have been carried by any local winds which were present. It is possible that with Bryn Farm on a higher ground above the Afon Tanat that at least some of virus could have been carried downward into the valley to the south. A number of farms in this area subsequently became infected. It is unlikely that there would have been a significant flow of air from Bryn Farm over the peak of the hill to the north-east of the farm. Any southerly flow being passed to the east or along the valley to the west of the hill.

## Summary

With the combination of the minimal virus release from the first two infected pigs and the light/calm winds it is likely that any subsequent infection would

Table 3. Lee-wave analysis

Date (Oct. 1967)	Wind speed > 15 kt nearly at right angles to the ridge	Presence of inversion or stable layer	Increase of wind speed with height	Initial forecaster assessment	'Caswell Method' assessment	Comments	Conclusion
21	No	Data not available	Data not available	Lee waves unlikely	n.a.	The lack of radiosonde data prevents any detailed analysis into the likelihood of waves on this day	In spite of no upper air data being available for this day, lee waves are considered highly unlikely due to the lack of any real strength in the wind flow
22	Yes	Data not available	Data not available	Lee waves unlikely	n.a.	The geostrophic wind on this day appears to only just reach 15 kt in strength. Cloud types being reported in the surface observations reflect a certain instability at low levels, which would not support lee waves	Marked lee waves were unlikely on this day
23	Yes	Yes	Yes	Lee waves likely	Negative /positive	Caswell's method initially gives a negative result when data from the Aberporth radiosonde is used. However, changing the wind direction slightly at 500 mb gives a positive result with a wavelength of 7.5 km and a maximum vertical velocity of 397 ft/min at 7000 ft. This illustrates the sensitivity of this method	Lee waves were likely during the morning but less likely after 1330 hours when the passage of the trough led to a decrease in surface winds
24	Yes	Yes	Yes	Lee waves likely	Positive	Caswell's method gives maximum vertical velocities of 591 ft/min at 4500 ft with a wavelength of 7.5 km	Lee waves were likely especially between 1100 and 1700 hours
25	Yes	Yes	Yes	Lee waves likely	Positive	Caswell's method gives maximum vertical velocities of 708 ft/min at 13 500 ft with a wavelength of 16 km. The height of 13 500 ft looks a little high as there appears to be a stable layer present between 6000 and 10 000 ft. Waves are more likely to be trapped below this	Lee waves were likely on this day between 0930 and 1320 hours
26	Yes	No	Yes	Lee waves unlikely	Negative	Although the winds are very strong there is strong evidence from the Aberporth Ascent that the atmosphere is very unstable from the surface through a deep layer	Lee waves were very unlikely on this day

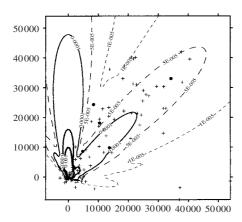


Fig. 4. Maximum hourly virus concentrations in TCID<sub>50</sub> m<sup>-3</sup>, for the period 21–26 October 1967 (Shawbury observations) together with the farm data presented in Figure 2b.

have been limited to the immediate area. It is highly unlikely that any lee waves were present due to the lack of any real strength in the wind flow.

#### 22 October

The midnight synoptic chart shows a definite north-westerly airflow affecting England and Wales with a weak ridge of high pressure extending north-east over East Anglia. By mid-day the wind had become south-westerly again with weak ridging evident in the isobars.

Surface winds recorded at Shawbury were a light south-westerly (typical direction 230° or 240°) with periods of calm between 0400 and 0800 hours. This is a good 50° different from the geostrophic wind, but cannot be considered that unusual because of the slackness and stability in the lowest layers of the atmosphere. The winds then backed to 190° after 1400 hours, but remained light throughout and exhibit the expected behaviour compared to the geostrophic flow above.

ADMS showed two distinctive plumes one to the north and the other to the north-east. The north-east plume being the stronger with the 0·00001 TCID<sub>50</sub> m<sup>-3</sup> contour extending north- eastwards to  $\sim 50$  km from the source and the 0·0001 TCID<sub>50</sub> m<sup>-3</sup> to  $\sim 10$  km. Within 1 or 2 km of the source values of 0·001 TCID<sub>50</sub> m<sup>-3</sup> are estimated.

Local topography is likely to have influenced the airflow especially if the periods of calm recorded at Shawbury were experienced at Bryn Farm. If the south-westerly winds were stronger then some flow would have at the very least passed up the valley to

the north-east of Bryn Farm, with some going over the peak.

## Summary

Overall livestock in the immediate vicinity of the farm were at greatest risk to challenge with airborne virus, but very low virus concentrations are likely to have been experienced a few tens of kilometres to the north-east. Lee waves are unlikely to have formed on this day.

## 23 October

A south-westerly airflow of some strength is the dominant feature on the midnight synoptic chart with the geostrophic wind direction approximately 240° over the West Midlands. Outbreaks of slight rain were reported at stations in West Wales. The surface winds being reported at Shawbury and Manchester are initially southerly (170°–190°) 7–10 kt, this backing and slackening effect being enhanced by nocturnal cooling. Closer examination of the daily register supports this as the surface wind veers from 180° to 230° between 0730 and 0900 hours. During the same period wind speed increased from a mean of 7–12 kt and an hour later to 16 kt.

On the midday analysis a trough has been analysed lying from Aberporth to Merseyside with outbreaks of rain being reported in West Wales. The wind flow remained a south-westerly of some strength with the geostrophic wind around  $250^{\circ}$ . Surface winds being reported at Shawbury averaged  $240^{\circ}$ , 18 kt until 1255 hours when they veered to  $270^{\circ}$  and dropped to a mean of  $\sim 11$  kt.

Whilst the virus release pattern is the same as on the previous day overall downwind concentrations calculated by ADMS are considerably lower; the prime reason for this being a combination of stronger wind speeds and a higher boundary layer depth during the middle of the day. The 0·00001 TCID<sub>50</sub> m<sup>-3</sup> contour only extended outwards to a maximum of 10 km in a sector north to north-east.

Local topography is unlikely to have played a major part, on this day, in modifying the overall air flow; the prime reason for this being the increased strength of the wind.

# Summary

Only livestock within 10 km of the source, in a sector north through to north-east would have been exposed to virus and for many of these concentrations would have been very low. Livestock at a greater distance or in a different direction are unlikely to have been exposed to airborne virus. Lee waves were likely during the morning but less likely after 1330 hours when the passage of the trough led to a decrease in surface winds.

#### 24 October

The midnight analysis again shows a reasonable strong south-westerly airflow (geostrophic wind direction 260°) with the trough which was over Wales at mid-day on the 23 October now lying from east Devon to Norfolk. As a consequence the West Midlands was under the influence of slightly different air to the previous day with surface reports indicating fairly dry conditions at low levels with large amounts of stratiform cloud. The surface winds at Shawbury and other local stations are well backed compared to the gradient wind with an average of 220°, 8 kt although this is not an unreasonable relationship to the gradient given the time of day and likely stability at low levels.

At mid-day the geostrophic flow remained westerly and of a reasonable strength. The surface flow being reported by Shawbury veered more south-westerly as the morning progressed, become westerly around 1300 hours before slowly backing south-westerly as evening approached. Surface wind speeds increased to maximum of 12 kt around midday and then became light as evening approached.

With an estimated second and third generation of pigs becoming infected at Bryn Farm the virus emission in to the atmosphere is significantly greater than on previous days. Consequently a greater likelihood of downwind infection is to be expected. ADMS supports this view. On this day downwind concentrations are calculated at their greatest of the entire emission period. The area at risk is once again predominantly in the sector north to east. The 0.00005 TCID<sub>50</sub> m<sup>-3</sup> contour covering the majority of the farms which became infected, the 0.0001 TCID<sub>50</sub> m<sup>-3</sup> contour extended outwards to ~25 km to the northeast and slightly further to the north. Maximum concentrations of  $\sim 0.005 \text{ TCID}_{50} \text{ m}^{-3}$  were calculated several kilometres to the north and north-east of Bryn Farm.

It is hard to determine just how much effect the local topography influenced the wind flow throughout this day. At the start of the day when winds were generally from around 210° it is likely that the air would have flowed from Bryn Farm up the valley to the north-east; during the hour when a calm wind was recorded it is not clear what would have happened. Around mid-day the wind speed increased and was much more westerly. As a result virus emitted from Bryn Farm would have travelled to the east. In the evening the wind had backed to southerly and as such virus emitted from Bryn Farm may once again have passed to the north.

#### **Summary**

The greatest risk of exposure to virus occurred on this day. Livestock at many kilometres to the north and north-east would have been challenged by airborne virus. Lee waves were likely especially between 1100 and 1700 hours.

#### 25 October

On the midnight synoptic chart a strong south-westerly airflow dominated (geostrophic wind 230°) ahead of a warm front lying from Dublin through the Llyn peninsula to Plymouth. By mid-day the majority of England appears to be in the warm moist air behind the warm front. The gradient appears to be unchanged in direction, but has strengthened considerably. A cold front passed from the west across Wales. Cumuliform cloud was reported over Ireland indicating increased destabilizing of the lower parts of the atmosphere.

The surface winds at Shawbury at the start of the day were around 190°, 8 kt at first, but increasing to a mean of 18 kt after 0930 hours and occasionally 20 or 21 kt in the afternoon. The direction remained fairly constant until it veered to around 220° when the cold front went through around 1323 hours. Cumuliform cloud was reported from 1525 hours, indicating increased instability in the atmosphere.

With virus emissions from the pigs at their peak it would be reasonable to expect that downwind virus concentrations would also be at a peak. ADMS and the meteorological analysis presented above do not support this view. The atmosphere was neutral to unstable for the majority of the day, winds were generally strong and as a result virus would have rapidly mixed vertically throughout the boundary layer. Consequently, downwind virus concentrations were significantly lower than on 24 October. The

 $0.00005~TCID_{50}~m^{-3}$  contour just extended to 40 km to the north and a second peak was evident to the north-east up to  $\sim 15$  km. The 0.0001 contour only extended to  $\sim 8$  km to the north and less to the north-east.

Due to the strength of the wind it is unlikely that topography played a significant role in modifying the observed airflow.

#### Summary

Overall on 25 October the likelihood of airborne virus challenge was less than on 24 October. That said, aerosol at very low concentrations would have passed over the majority of farms which subsequently became infected. Lee waves were likely on this day between 0930 and 1320 hours.

#### 26 October

A very strong south-westerly airflow is evident on the midnight chart with a geostrophic wind of 250°. By mid-day this veered to 270° but its strength remained very strong. On both charts surface winds in the Shropshire and Cheshire area are being reported as very strong with moderate to large cumuliform cloud and showers indicating fairly high degrees of instability to be present.

The daily register for Shawbury confirms the surface winds as being a strong south-westerly, averaging 220°–250°, 19–25 kt, much as expected compared to the gradient wind. Cumulus cloud is reported at the outset with some Cumulonimbus cloud present after 1600 hours.

ADMS clearly identifies a single area of risk to the north-east of Bryn Farm. The 0·00005 contour extending to  $\sim 30 \text{ km}$  and the 0·0001 TCID<sub>50</sub> m<sup>-3</sup> to  $\sim 8 \text{ km}$ . Once again the majority of farms which subsequently became infected are contained within this footprint.

Due to the strength of the wind it is unlikely that local topography played a significant role in modifying the observed airflow.

## Summary

Overall livestock to the north-east of Bryn Farm would have been exposed to very low concentrations of virus. The nearer the source the greater the potential challenge. Lee waves were very unlikely on this day.

#### DISCUSSION

Hugh-Jones & Wright [8] analysed the initial spread of FMD from Bryn Farm and suggested that weather played a major part. The analysis in this paper is in close agreement with their findings on spread of FMD from Bryn Farm by wind.

The findings of these investigations indicate that FMD virus emitted by infected pigs on Bryn Farm (primary outbreak) could have infected the 12 farms north-east of Bryn Farm within 5 km (phase 2a) and the 16 farms 16-54 km north-east of Bryn Farm (phase 2b) by the airborne route. If other sources of infection for farms are excluded 10 of the 12 farms (phase 2a) and 12 of the 16 farms (phase 2b) would have been infected by the airborne route. The cattle on two farms north-east of and close to Bryn Farm had lesions of FMD on 27 October [8] and could have been a source of infection for up to four farms within 5 km of Bryn Farm and further to the north-east that had lesions on 31 October and 1 November. However, the virus output from the cattle would have been less than that from the pigs at Bryn Farm. Thus, no other source than that by the airborne route can be ascribed to six farms north-east and within 5 km of Bryn Farm (phase 2a) and 12 farms 16–54 km north-east of Bryn Farm (phase 2b).

Farms with disease confirmed between 2 and 5 November (phase 3) around Bryn Farm and up to 60 km north-east of Bryn Farm could have been infected from Bryn Farm by the airborne route. However, during this period there could have been secondary spread from the four farms, which had contact with Argentine lamb meat or bones (phase 2b). In addition there could have been tertiary spread from those farms previously infected from Bryn Farm (phases 2a and 2b). It is not possible to distinguish with certainty which outbreaks were secondary and which were tertiary. This difficulty was also experienced by Wright [12].

The results from the ADMS model indicate that livestock on the majority of farms that became infected would have been challenged by airborne virus. However, away from the immediate source, airborne virus concentrations are calculated as being significantly less than those estimated from laboratory investigations to cause infection. This effect can be clearly seen in Figure 4. A significant percentage of farms in the range 5–40 km from the source were exposed to maximum hourly concentrations of between 0.0001 and 0.00005 TCID<sub>50</sub> m<sup>-3</sup> compared to that

estimated to infect in the laboratory (0.06-0.07 TCID<sub>50</sub> m<sup>-3</sup>). This finding is very consistent with findings from a number of other studies [33, 34]. The reason for this difference requires clarification. Could it be that the calculations of concentrations averaged over a period of time are not the best predictor of disease spread? If not, could the incidence of disease spread, under certain atmospheric conditions, be more influenced by the ability of the particlecontaining virus to remain airborne and viable? In other words the optimum conditions for long-distance spread of disease may occur when the wind is strong and the atmospheric stability close to neutral. Highly unstable air may dilute the downwind concentration to such an extent that the chance of infection is minimized. More local spread may still be more likely under stable atmospheric conditions when plume concentrations are significantly higher and the overall chance of an animal inhaling an infected particle is greater. Other possibilities of explaining the difference between model calculations and laboratory findings include an uncertainty of just how much virus is emitted by infected animals and the minimum amount of virus required to infect susceptible animals by the airborne route; inaccurate model representation of what is happening particularly close to the virus source or that laboratory observations do not mimic field conditions. A targeted research programme has recently been commissioned by Defra, based at the Institute for Animal Health, Pirbright Laboratory to untangle some of the issues raised above. The results of which are eagerly awaited.

The analysis presented in this paper suggests that there were periods coincident with the release of virus from Bryn Farm when the atmospheric conditions were suitable for the formation of lee waves. This finding is in agreement with that of Tinline [9]. There is agreement that these conditions were present on 25 October, coincident with the maximum virus release from the infected pigs. Our analysis suggests that conditions were also suitable on 23 and 24 October. However, there is disagreement concerning lee-wave formation on 26 October. The analysis, based on the Aberporth ascent and observed cloud types indicates that the atmosphere was unstable at a high altitude and as a consequence organized waves would have been very unlikely. It is recognized, however, that the winds were very strong and undoubtedly turbulent throughout the day.

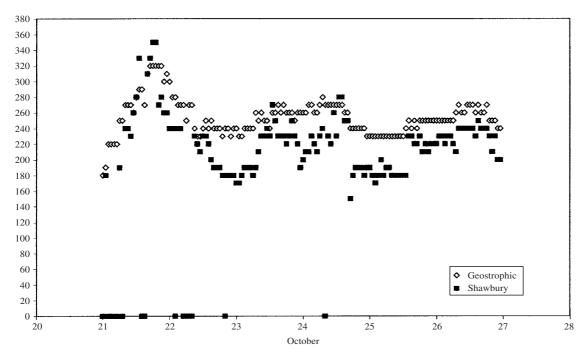
Given the general agreement that that lee waves were likely for periods on at least one of the days of interest it is necessary to establish whether, as Tinline [9] suggests, there was a 'volumetric concentration' of virus at locations in areas of downward airflow and if this was the case could it have increased the likelihood of infection. The present authors believe this to be unlikely for a number of reasons.

First, given the strength of wind, the nature of the terrain and the stability of the atmosphere it is likely that virus emitted from Bryn Farm would have quickly dispersed throughout the depth of the boundary layer. Any strong downwards and upwards mixing of air to the east of the mountains, associated with any lee waves, would have helped to ensure that the mixing process was very thorough. Consequently it is unlikely that livestock at a given location would have been exposed to significant increases in virus concentrations caused by any virus contained in downdraughts.

Second, it has now been established that infection is significantly less likely through ingestion than through inhalation (see Introduction). Any virus particles that were brought to the surface by down currents had the potential for being deposited to the surface, thus decreasing the risk of infection rather than increasing it.

Third, Tinline [9] suggested that the location of secondary outbreaks was consistent with the calculated lee-wave lengths. For a given mountain range it is extremely difficult to estimate the location and orientation of lee waves. It is necessary to establish which part of the mountain actually triggers the formation of any waves. In the Oswestry case was it the presence of the significantly higher ground around 40 km to the west, the edge of the hills around Oswestry or somewhere in between? The orientation is also difficult to estimate. Should the waves be parallel to the mountain edge (generally north to south in this particular case) or aligned with the wind direction? Bradbury [44] suggests that waves generally form parallel to the alignment of major ridges and not necessarily at right angles to the flow. A close examination of the locations of the infected farms (Fig. 2a, b) does not appear to shed any light on these questions. The outbreaks would appear to be generally dispersed throughout the sector to the north-east of Bryn Farm, rather than along distinctive lines.

Whilst the authors believe that the pattern of downwind infection of livestock can be described using dispersion theory the study has shown that there is very limited published work on the impact of lee waves on the dispersion of airborne material.



**Fig. 5.** Comparison of Shawbury 10-m wind direction with the geostrophic wind for the period 21–26 October 1967. The wind blew predominantly from the south and south-west.

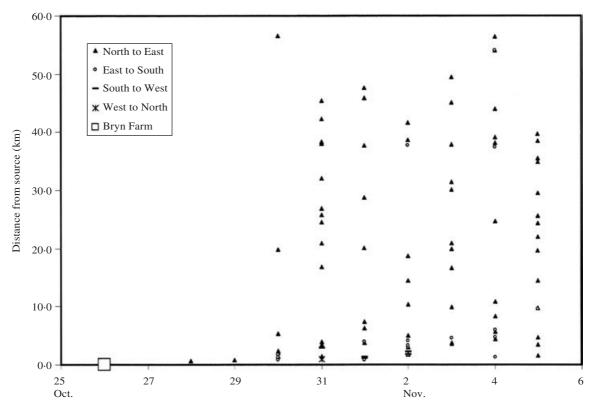
Shawbury wind observations have been used in this paper as a prime source of data for input to the dispersion model. Is the use of this data, taken 30 km east of Bryn Farm (156 m) on the Cheshire Plain appropriate to virus released near Oswestry, where the ground rises steeply from ~100 m to 400 m at 6 km and up to 827 m further to the west? It is the authors' view that given the conditions covered by this investigation Shawbury data are generally representative of large-scale synoptic airflow movements. Apart from 21 October when the winds were very light and variable in direction and local topographical effects are likely to have influenced the airflow there was good agreement between the surface wind direction observations. Over the period 22-26 October wind directions ranged from 160° to 280° and at any hour individual stations rarely differed by more than 30°. However, it is believed that given medium to strong, south-westerly or westerly winds Shawbury data are likely to underestimate the wind speed at Bryn Farm. Clearly on the Cheshire Plain they are more likely to represent actual conditions.

Figure 5 gives a comparison between Shawbury and the geostrophic wind. In general the Shawbury observation is between 20° and 60° backed from the geostrophic wind. If the airflow at the exposed Bryn Farm was closer to the geostrophic wind then virus emitted would have started its track in a different

direction to that suggested using Shawbury data. For example on 25 October the wind direction would have been around 230° rather than 180° suggested by Shawbury and 250° rather than 220° during the early hours of 26 October. To quantify the effect of the geostrophic wind on the resultant virus plume track ADMS was re-run but with the Shawbury wind direction replaced by the geostrophic wind direction. All other inputs were kept constant. The results confirmed that the area at risk was shifted clockwise by about 50° with the magnitude of the concentrations being similar to those given in Figure 4.

It is possible that virus particles emitted from Bryn Farm could have taken a curved trajectory, starting in a direction somewhere between the surface and geostrophic wind directions and then followed the direction indicated by the surface stations such as Shawbury, Lyonshall and Clee Hill. Whether the simple wind direction of Shawbury or the more complex, but plausible, curved trajectory is used, virus emitted from Bryn Farm would have been carried to the sector between north and east.

During the 2001 UK FMD epidemic there was significant discussion concerning the time taken to bring the epidemic under control, in particular the introduction of movement controls. Whilst it is readily recognized that many of the factors that influence such decisions fall well outside the scope of this paper



**Fig. 6.** Date of confirmation of disease and distance from Bryn Farm. Each outbreak has been divided into one of four sectors (north to east, east to south, south to west and west to north).

it is useful to consider what advice could have been available to those responsible for disease control in 1967, based upon our current understanding of disease spread. Assuming that good communication links existed between MAFF, Pirbright and the Met Office a preliminary risk assessment could have been available within hours of the disease/virus information becoming available and detailed advice, based on a range of numerical models, within 48 h. If the virus strain was initially unknown then a worst-case emission scenario could have been used. Based on the clinical examination findings this would have shown that the risk of airborne disease spread was within a ring 5 km around the source, but with a strong possibility of further infections to the north and north-east. The extension of this risk area to the north and north-east being 30-40 km; the chance of infection beyond this distance could not be ruled out. Areas to the west and south would be defined as low or minimum risk. This information could have been of valuable input to those responsible for disease control, in particular with regard to targeting limited resources and selecting areas of movement restriction.

The merit or otherwise, of introducing ring or emergency vaccination was also a matter of much discussion in the 2001 UK epidemic. The subject is likely to be at the forefront of disease controllers minds when the next outbreak occurs in the United Kingdom. One of the factors controllers need to take into account is the potential for airborne disease spread. Are there any lessons to be learnt from the start of the 1967–1968 epidemic? To explore this matter it is important to re-create the unfolding disease scenario. For each farm included in this study the date of confirmation of disease, its distance from Bryn Farm and its geographical location (north to east, east to south, south to west or west to north) were plotted (Fig. 6). It can be seen that on 30/31 October, there was a sudden explosion of outbreaks, predominately in the vicinity of the source and 55 km out to the north-east. The occurrence of disease to the south and west being minimal. Given this rapidly unfolding scenario would the introduction of a vaccination programme help to control disease spread? Assuming that many of the pigs became infected during the period 24–26 October then vaccination after this date would not have prevented disease from being seeded over a large area. By vaccinating in the high-risk area it may have been possible to reduce the next generation of infection. However, if the vaccination programme was delayed until early November then secondary and tertiary infection would have occurred. An alternative strategy could have been to vaccinate livestock in the low or minimal risk area, thus preventing them from becoming infected. Two clear lessons emerge from the study. First, the importance of early recognition of disease. If disease had been confirmed as early as 24 October and the pigs slaughtered then airborne spread of virus from the farm would have been minimal and the likely scale of the outbreak minimized. Second, a high degree of preparedness is required if vaccination is likely to be beneficial – any delay in implementing a decision could have serious implications on its chances of success.

It is interesting to compare the starts of the 1967-1968 and 2001 UK epidemics. Both epidemics recorded in excess of 2000 FMD cases. In the 1967–1968 instance the number of infected animals (pigs) was small, the airborne virus released passed over a very dense and susceptible animal population (approximately 60 cattle per 100 acres) [4] and there was little movement of livestock. In the 2001 UK epidemic there were significantly more pigs excreting airborne virus and whilst the plume passed over some nearby cattle and sheep, causing infection, for much of the period it would have travelled over or in the vicinity of the city of Newcastle and then out to sea. In the 2001 UK epidemic there was significant movement of sheep [45]. It is clear that whilst both epidemics were on the same scale it was the combination of circumstances which influenced the course of the epidemic. To help those responsible for disease control to weigh up each of the factors and their significance in the next outbreak it is important to have an accurate, timely assessment of all of the factors including the potential for airborne spread. Gloster [46] and Alexandersen [47] identify the individual components which influence the accuracy of disease prediction and the current areas of uncertainty. It is readily recognized that there is still some way to go in perfecting the forecasting technique. In the first instance a prediction of risk from airborne disease spread can be made using a worst-case scenario based on the strain with the maximum output and the smallest concentration downwind which has been found to infect animals derived from this, previous and future studies. This may be of very limited use to those responsible for disease control. The overall direction of the area of risk is likely to be correct, but the likely distance for infection would be far from precise.

Consequently, decisions taken at an early stage may subsequently be shown to be in error. To minimize this shortcoming it would be prudent to have information on aerosol production and the dose required to infect by the respiratory route for all of the relevant known circulating virus strains readily available. It may be possible to develop a portable particle virus sampler which could be used in the field at the time of diagnosis. This could provide highly important information. A more realistic estimate may subsequently be made through laboratory measurements. However, the results from these experiments may not be available for a number of weeks after the start of the outbreak.

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# REFERENCES

- 1. **Defra/Department of Culture, Media and Sport.** Economic costs of foot-and-mouth disease in the UK a joint working paper (2002), submitted to the Foot-and-mouth disease 2001: Lessons to be learned inquiry report 2002. London: The Stationery Office.
- 2. **Royal Society.** Policy document 15/02. Infectious diseases in livestock, 2002 (www.royalsoc.ac.uk).
- 3. **Thompson D, Muriel P, Russell D, et al.** Economic costs of the foot and mouth disease outbreak in the United Kingdom in 2001. Rev Sci Tech 2002; **21**: 675–687.
- Report of the Committee of Inquiry on foot-and-mouth disease 1968. Part 1. London: HMSO, April 1969.
- 5. **Penberthy J.** Foot-and-mouth disease. J Comp Path Ther 1901; **24**: 16–29.
- 6. **Bang B.** Foot-and-mouth disease. J Board Agriculture 1912; **19**: 624–647.
- 7. **Bang B.** Foot-and-mouth disease. J Comp Path 1912; **25**: 1–15.
- 8. **Hugh-Jones ME, Wright PB.** Studies on the 1967–8 foot-and-mouth disease epidemic, the relation of weather to spread of disease. J Hyg (Camb) 1970; **68**: 253–271.
- 9. **Tinline RR.** Lee wave hypothesis for the initial pattern of spread during the 1967–68 foot-and-mouth epizootic. Nature 1970; **227**: 860–862.
- 10. **Report on the Animal Health Services in Great Britain.** Foot-and-Mouth Disease: the 1967–1968 epidemic.

- Ministry of Agriculture, Fisheries and Food. HMSO: London, 1967; 13–19.
- Report on the Animal Health Services in Great Britain. Foot-and-Mouth Disease. Ministry of Agriculture, Fisheries and Food. HMSO: London, 1968; 8–20.
- Wright PB. Effects of wind and precipitation on the spread of foot-and-mouth disease. Weather 1969; 24: 204–213.
- 13. Alexandersen S, Zhang Z, Donaldson AI, et al. The pathogenesis and diagnosis of foot-and-mouth disease. J Comp Pathol 2003; 129: 1–36.
- Sellers RF, Parker J. Airborne excretion of footand-mouth disease virus. J Hyg (Camb) 1969; 67: 671– 677
- Donaldson AI, Herniman KA, Parker J, et al. Further investigations on the airborne excretion of foot-and-mouth disease virus. J Hyg (Camb) 1970; 68: 557-564
- Donaldson AI, Ferris NP, Gloster J. Air sampling of pigs infected with foot-and-mouth disease virus: comparison of Litton and Cyclone samplers. Res Vet Sci 1982: 33: 384–385.
- 17. **Alexandersen S, Brotherhood I, Donaldson AI.** Natural aerosol transmission of foot-and-mouth disease virus to pigs: minimal infectious dose for strain O1 Lausanne. Epidemiol Infect 2002; **128**: 301–312.
- 18. Alexandersen S, Quan M, Murphy C, et al. Studies of quantitative parameters of virus excretion and transmission in pigs and cattle experimentally infected with foot-and-mouth disease virus. J Comp Pathol 2003; 129: 268–282.
- 19. **Alexandersen S, Donaldson AI.** Further studies to quantify the dose of natural aerosols of foot-and-mouth disease virus for pigs. Epidemiol Infect 2002; **128**: 313–323.
- Donaldson AI. The influence of relative humidity on the aerosol stability of different strains of foot-and-mouth disease virus suspended in saliva. J Gen Virol 1972; 15: 25–33
- Donaldson AI, Gibson CF, Oliver R, et al. Infection of cattle by airborne foot-and-mouth disease virus: minimal doses with O1 and SAT 2 strains. Res Vet Sci 1987; 43: 339–346.
- 22. Sørensen JH, Mackay DK, Jensen CO, Donaldson AI. An integrated model to predict the atmospheric spread of foot-and-mouth disease virus. Epidemiol Infect 2000; 124: 577–590.
- Donaldson AI, Alexandersen S. The relative resistance of pigs to infection by natural aerosols of foot-and-mouth disease virus. Vet Rec 2001; 148: 600–602.
- Alexandersen S, Zhang Z, Reid SM, et al. Quantities of infectious virus and viral RNA recovered from sheep and cattle experimentally infected with foot-and-mouth disease virus O UK 2001. J Gen Virol 2002; 83: 1915–1923.
- Ryall D, Maryon RH. Validation of the UK Met Office's NAME model against the ETEX dataset. Atmos Environ 1998; 32: 4265–4276.

- Malcolm AL, Derwent RG, Maryon RH. Modelling the long range transport of secondary PM<sub>10</sub> to the UK. Atmos Environ 1999; 34: 881–894.
- Manning AJ. Predicting NO<sub>x</sub> levels in urban areas using two different dispersion models. Proceedings of the Sixth International Conference on Harmonisation within Atmospheric Dispersion Modelling for Regulatory Purposes, 1999.
- 28. Carruthers DJ, Holroyd R J, Hunt JCR, et al. UK-ADMS a new approach to modelling dispersion in the Earth's atmospheric boundary layer. J Wind Eng and Ind Aero 1994; **52**:139–153.
- Mikkelsen T, Larsen SE, Thykier-Nielsen S. Description of the Risø puff diffusion model. Nuclear Tech 1984: 67; 56–65.
- Mikkelsen T, Thykier-Nielsen S, Astrup P, et al. MET-RODOS: a comprehensive atmospheric dispersion module. Radiat Prot Dosim 1997; 73: 45–56.
- 31. Sørensen JH, Jensen CO, Mikkelsen T, et al. Modelling the atmospheric dispersion of foot-and-mouth disease virus for emergency preparedness. Phys Chem Earth 2001; 26: 93–97.
- Sørensen JH. Sensitivity of the DERMA longrange dispersion model to meteorological input and diffusion parameters. Atmos Environ 1998; 32: 4195– 4206.
- 33. Gloster J, Champion HJ, Sørensen JH, et al. Airborne transmission of foot-and-mouth disease virus from Burnside Farm, Heddon-on-the-Wall, Northumberland during the 2001 UK epidemic. Vet Rec 2003; 152: 525–533
- 34. Mikkelsen T, Alexandersen S, Champion HJ, et al. Investigation of airborne foot-and-mouth disease virus transmission during low-wind conditions in the early phase of the UK 2001. Epidemiol Atmos Chem and Phys Discus 2003; 3: 677–703.
- 35. Alexandersen S, Kitching RP, Mansley LM, et al. Clinical and laboratory investigations of five outbreaks during the early stages of the 2001 foot-and-mouth disease epidemic in the United Kingdom. Vet Rec 2003; 152: 489–496.
- 36. **Tinline RR.** Meteorological aspects of the spread of foot-and-mouth disease: evidence from the 1967–68 epizootic in the English Midlands. Read at 5th International Biometric Congress; September 1969.
- Sørensen JH, Jensen CO, Mikkelsen T, et al. Modelling the atmospheric dispersion of foot-and-mouth disease virus for emergency preparedness. Epidem Infect 2000; 124: 577–590.
- 38. Sellers RF, Herniman KAJ, Donaldson AI. The effect of killing or removal of animals affected with foot-and-mouth disease on the amounts of airborne virus present in looseboxes. Brit Vet J 1971, 127: 358–365.
- 39. **Sellers RF, Foreman AJ.** The Hampshire epidemic of foot-and-mouth disease. J Hyg (Camb) 1967; **67**: 671–677.
- 40. **Anon.** Foot and mouth disease. Ageing of lesions. Reference book 400. HMSO: London, 1986.

- 41. Meteorological Glossary. Met O985; HMSO, 1991.
- 42. **Caswell SA.** A simplified calculation of maximum vertical velocities in mountain lee waves. Met Mag 1966; **95**: 68–80.
- 43. Gloster J, Champion HJ, Mansley LM, et al. The 2001 epidemic of foot-and-mouth disease in the United Kingdom: epidemiological and meteorological case studies. Vet Record (in press).
- 44. **Bradbury T.** Meteorology and flight. A & C Black Ltd, 1989.
- 45. **Mansley LM, Dunlop PJ, Whiteside SM, et al.** Early dissemination of foot-and-mouth disease through sheep marketing in February 2001. Vet Rec 2003; **153**: 43–50.
- 46. **Gloster J, Esteves I, Alexandersen S.** Moving towards a better understanding of airborne transmission of FMD. EU FMD Presentation & Conference Proceedings, Crete, October 2004: Appendix 36.
- 47. **Alexandersen S, Gloster J.** Airborne transmission of foot-and-mouth disease. Aerosol Society Newsletter 2004; **42**: 4–9.