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# Predicting infection risk of airborne foot-and-mouth disease

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Foot-and-mouth disease is a highly contagious disease of cloven-hoofed animals, the control and eradication of which is of significant worldwide socio-economic importance. The virus may spread by direct contact between animals or via fomites as well as through airborne transmission, with the latter being the most difficult to control. Here, we consider the risk of infection to flocks or herds from airborne virus emitted from a known infected premises. We show that airborne infection can be predicted quickly and with a good degree of accuracy, provided that the source of virus emission has been determined and reliable geo-referenced herd data are available. A simple model provides a reliable tool for estimating risk from known sources and for prioritizing surveillance and detection efforts. The issue of data information management systems was highlighted as a lesson to be learned from the official inquiry into the UK 2007 foot-and-mouth outbreak: results here suggest that the efficacy of disease control measures could be markedly improved through an accurate livestock database incorporating flock/herd size and location, which would enable tactical as well as strategic modelling.

**Keywords: epidemiology; modelling; risk; foot-and-mouth disease**

## 1. INTRODUCTION

Foot-and-mouth disease (FMD) is a highly infectious disease of cloven-hoofed animals, which can be transmitted by direct contact, fomites or through the air. It is of enormous social and economic importance both in regions of the world where it is endemic and in those countries considered disease free by the OIE (World Organisation for Animal Health). In addition to the impact of FMD on animal welfare and productivity, the loss of disease-free status results in costly trade restrictions. Its social and economic impacts—as witnessed in the UK in 2001 (Anderson 2002)—are considered sufficient to justify stringent control measures including the implementation of a stamping-out policy. In addition to this, control within the European Union involves movement restrictions, the imposition of control and surveillance zones and an obligation to consider the use of emergency vaccination.

While most secondary foot-and-mouth virus (FMDV) transmission between premises can, in theory at least, be prevented or at least controlled by stringent on-farm bio-security precautions and rigorous investigations of all movements on and off the infected premises, it is difficult to control airborne transmission. Airborne transmissions have been recorded up to 50 km overland (Hugh-Jones & Wright 1970; Gloster *et al.* 2005) and over 200 km over water (Donaldson *et al.* 1982; Gloster *et al.* 1982). Consequently, it is very important in the control of any outbreak to be able to both accurately and speedily identify livestock that are at risk to airborne virus. Although such transmission might be reduced by appropriate animal housing, it cannot be blocked in the same way that direct contact (through movement restrictions) or fomite transport (through thorough disinfection) can. It should be noted, however, that speed is essential if accurate prediction of airborne transmission is to contribute to the control and prevention of transmission and successful eradication of disease.

In this paper, a simple model of infection risk, as a result of exposure to airborne virus emitted from a known source, is developed for herds and flocks. Parameters are fitted to a previous outbreak where a detailed record of suspected transmission pathways based on extensive tracing and investigation is available. Results are then applied to a more recent outbreak in order to evaluate the model as a predictive tool: explicitly, the expected infection risk from a number of different potential virus sources was calculated for all surrounding herds and then compared with their recorded outcome.

### *1.1. Hampshire (UK) 1968 outbreak*

On 6 January 1968, a series of outbreaks involving O1 BSF1860 virus strain commenced in Hampshire, UK, when disease was confirmed in the cattle at Southwick.

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The disease was subsequently confirmed on 29 farms and 2774 cattle, 414 sheep, 4708 pigs and 6 goats were slaughtered (Report of the Animal Health Services in Great Britain 1967). A detailed epidemiological investigation concluded that disease was likely to have commenced towards the end of December 1966. The study also identified how each farm is believed to have become infected; this included 16 farms that were likely to have been infected by airborne transmission, 12 of which from the local abattoir (Sellers & Forman 1973). The data on all infected premises associated with the outbreak were collected, while information on uninfected premises was recorded only for those close to the abattoir.

### 1.2. Surrey (UK) 2007 outbreak

In 2007 a case of FMD on a cattle farm in Normandy, Surrey, UK, was confirmed on 3 August 2007 (Defra 2007*a*), the first FMD outbreak in the UK since 2001 (Defra 2007*a*,*b*; Anderson 2008). Infection was detected nearby on a second farm on 6 August (Defra 2007*a*). On 12 September, FMD was confirmed on a third farm approximately 20 km from Normandy in Egham, followed by five more outbreaks in that area in the next three weeks (Defra 2007*a*,*b*; Anderson 2008). A total of 1578 animals were culled on infected farms, of which FMDV infection was confirmed in 238 by detection of viral antigen, genome or antibodies to FMDV (Defra 2007*b*; Ryan *et al.* 2008). Post-outbreak surveillance provided the details and locations of all premises with livestock within 10 km of any infected premises.

## 2. METHODS

Over the years, a number of numerical models to estimate the downwind concentration of FMDV particles have been developed. These have been adapted from existing models, developed to provide guidance to emergency response planners in areas such as nuclear accidents, volcanic eruptions, major chemical releases and airborne carriage of bluetongue-infected midges. One of these, the UK Met Office's Numerical Atmospheric-dispersion Modelling Environment (NAME; Jones *et al.* 2007) has been used in this study; NAME is a Lagrangian particle model that has been used to provide guidance to the Department for the Environment, Food and Rural Affairs (Defra), and its predecessors, since the 1980s. Virus emissions from infected animals are represented by releasing a large number of particles, each of which carries a small proportion of the total virus released, into a model of the atmosphere. These particles subsequently follow stochastic trajectories (to represent the influence of mean wind and atmospheric turbulence on their transport) in a model atmosphere driven by appropriate input meteorology.

### 2.1. Emission model

For both of the Hampshire 1968 and Surrey 2007 outbreaks, virus emission profiles were constructed from veterinarians'/epidemiologists' reports made at the infected premises (Sellers & Forman 1973; Ryan *et al.* 2008); these are based on a close examination of the infected animals, together with knowledge of virus emissions measured under laboratory conditions. The ageing of FMD lesions by experienced examiners is thought to be accurate to plus or minus 1 day up to 5 days, but thereafter accuracy decreases (Anon 1986).

The disease has an incubation period ranging from 1 to 14 days, which is related to the infectious dose received (Alexandersen *et al.* 2003), with a farm-to-farm incubation period following airborne spread of 4–14 days (Sellers & Forman 1973). The most likely incubation period for FMDV strain O1 BFS infection of cattle is 2–5 days (Anon. 1969). Laboratory results show that individual pigs excrete O1 BSF1860 for a period of 4 or 5 days, commencing at very low levels on the day prior to the detection of the first clinical signs, reaching a maximum on the first and second day and then reducing substantially over the next 2 days (Sellers & Parker 1969). These values are used to produce a profile of expected level of virus emission from each source premises over time.

### 2.2. Dispersion model

Meteorological data, relevant to the locations of the infected premises, are then input to NAME. For the Hampshire case, meteorological observations from nearby recording stations at Thorney Island and RAF Calshot were used to drive NAME. In the more recent Surrey outbreak, gridded meteorological data at a horizontal resolution of 4 km from the Met Office's numerical weather prediction model, the unified model (Davies *et al.* 2005), were available.

NAME was run separately for each source premises over the relevant days and output was generated in the form of a time series of hourly integrals of the concentration of (virus) particles at each farm location ($\mathrm{TCID}_{50}\,\mathrm{m}^{-3}$).

### 2.3. Infection model

Risk of infection was based on the consideration of a herd of $n_{ij}$ cattle on farm $i$ exposed to a mean dose $d_{ij}$ during time interval $t_{ij}$ (thus, $i$ is the location index and $j$ is the time index). In what follows, we use the same length time steps of 1 hour on all premises ($t_{ij}=t_j=1$ hour for all $i$), so that $d_{ij}$ is the mean dose during the $j$th hour after virus was first emitted from the source. The probability $p_{ij}^k$ that an individual animal on that farm will take up $k$ infective doses during this time follows a Poisson distribution,

$$p_{ij}^k = \frac{(\theta d_{ij} t_{ij})^k}{k!}\mathrm{e}^{-\theta d_{ij} t_{ij}}.$$

Here, $\theta$ is the expected number of infective doses an animal is expected to take up per unit time per unit of exposed dose, which is generally unknown. The probability that an individual remains uninfected (i.e. takes up no doses) is $q_{ij}=p_{ij}^0$. Assuming that the herd is housed in a sufficiently open environment, so that the amount of air resampled by different animals is negligible, the probability of all animals in the herd remaining uninfected is $Q_{ij}=(q_{ij})^n$. Finally, the probability of the herd becoming infected at some point during the emission time interval $[0,T]$, the combined time span of all the individual time steps $\{t_{ij}\}_j$, is $P_i=1-\prod_j Q_{ij}$. For the standard case, where the herd size does not change over time ($n_{ij}=n_i$ for all $j$) this reduces to $P_i=1-\mathrm{e}^{-\theta d_i n_i}$, where $d_i=\sum_j d_{ij}t_{ij}$ is the total dose over $[0,T]$; as $t_{ij}\to 0$, we attain the limit $d_i=\int_0^T D_i(t)\mathrm{d}t$, where $D_i(t)$ is the continuous dosage profile at the location of farm $i$.

The simplest model for the dosage is to assume that this is equivalent to the current air concentration of virus $c_{ij}$, and that this is proportional to the concentration of particles present $s_{ij}$, which were emitted from the source. Setting $s_i$ as the cumulative total for the concentration of particles emitted from the source which are present at location $i$ over time $[0,T]$, the probability that the herd at farm becomes infected is

$$P_i(\theta)=1-\exp(-\theta s_i n_i),$$

rescaling $\theta$ as necessary. Here, the single parameter $\theta$ consolidates a number of (often species specific) factors including animal lung capacity and breathing rate, the proportion of emitted particles that contain virus and the necessary dosage for infection; the explicit inclusion of each is therefore not required, something of necessity in the case of those parameters that are unknown or not easily quantified.

Using the transmission routes from the main source for the Hampshire 1968 outbreak, as found by Sellers & Forman (1973), the maximum-likelihood estimate $\hat{\theta}$ was calculated, based on suspected airborne transmissions to cattle only: infected herds where an alternative route or source was deemed more likely were excluded, since it is unclear whether these could also have been subject to airborne infection or would have remained uninfected otherwise. The likelihood function is given by

$$L(\theta)=\prod_{i\in I}P_i\prod_{i\in U}Q_i,$$

where $I$ is the set of all herds suspected of having been infected by airborne transmission; $U$ is the set of all uninfected herds; and $Q_i=1-P_i$. Explicitly, $\hat{\theta}$ was found by minimizing $L(\theta)$ through Matlab's fminsearch procedure.

For each farm in the area, we therefore derive an expected probability of infection $\hat{P}_i=P_i(\hat{\theta})$ and, considering all recorded farms, we derive the probability threshold $P^*$ (above which we suspected a farm to be infected) by equalizing the sensitivity and specificity of the test applied to all herds in $I\cup U$. This choice was considered the best balance between the added value of predicting undetected infected premises with the potential harm of misdirecting resources to uninfected premises, although in future sensitivity could be prioritized at the expense of specificity, or vice-versa, if considered appropriate. In practice, owing to the greater number of uninfected premises compared with infected premises, there is often a range of values of $P^*$ yielding the same sensitivity but with differing specificity, and we therefore maximize the specificity within this range (see figure 1 for details). These results were then applied directly to the Surrey 2007 outbreak. Note that the union $I\cup U$ does not include those premises that became infected but for which the source was uncertain, since it is unclear how results for these should be weighted. Inclusion of premises where airborne transmission could not be ruled out (but was considered unlikely) results, as we would expect, in a model with increased sensitivity but significantly reduced specificity.

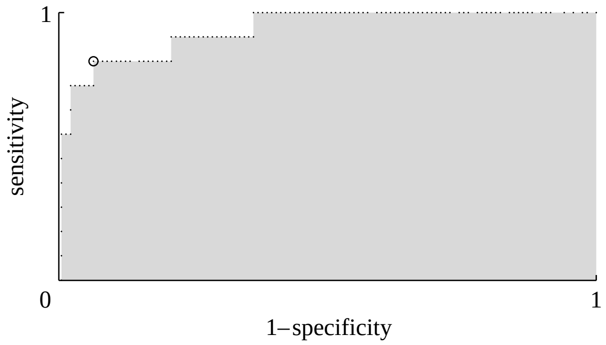

Figure 1. The receiver operating characteristics curve for the model test, showing its sensitivity and specificity as the value of $P^*$ is varied. For each possible value of sensitivity (relating to the 11 infected cases), there is usually a range of specificity values from which the highest is selected; the point relating to the chosen value $p^*=1.749\times10^{-1}$ is highlighted with a circle. The area under the curve (grey shaded) is greater than 0.94, suggesting that it is an excellent test when applied retrospectively to the Hampshire outbreak data.

Molecular epidemiological tracing is useful in determining transmission routes between premises (Cottam *et al.* 2006). Such an analysis of all premises involved in the Surrey 2007 outbreak has provided details of the virus transmission pathways, indicating both which infected premises were associated with each other and the chronology of infection (Defra 2007*a*; Cottam *et al.* 2008). Combining the molecular analysis (Defra 2007*a*; Cottam *et al.* 2008), the tracing of animal and human movements (Defra 2007*a*) and the inspection of animals on infected premises (Ryan *et al.* 2008) allow the relationships between infected premises to be classified into three groups: unrelated premises (where transmission of virus between premises was considered impossible or highly unlikely); possible airborne transmission (where there was a viral relationship between premises but an alternative transmission route had been identified); or an airborne transmission was assumed to have occurred (where the viral relationship between premises could not be explained by other means): these are summarized in table 1. The possibility of airborne introduction of virus has also been considered independently for all outbreaks (Gloster & Burgin 2007).

## 3. RESULTS

### *3.1. Hampshire 1968 fitted model*

Outcomes for the model fitted to the outbreak are shown in figure 2, with the size of points plotted related to the expected risk of infection of the farm they

Table 1. Suspected relationship of premises involved in the Surrey UK 2007 outbreak. (IP, infected premises; for derivation see text.)

| | premises classified as potentially having been infected by the source | |
|---|---|---|
| premises classified as a possible source of virus transmission | through airborne transmission | through a different route |
| IP1b | IP2b IP2c | |
| IP2b | | IP4b IP5 |
| IP3b | IP6 IP7 | IP8 |
| IP4b | IP3b | IP3c |
| IP6 | | IP7 IP8 |
| IP7 | IP8 | |

represent: for O1 BSF1860 transmission to cattle (based on an emission profile for pigs) the expected rate was $\hat{\theta}=7.44\times10^{-2}$ animal$^{-1}$ (TCID$_{50}$ m$^{-3}$)$^{-1}$, with a 95% CI of $(3.54\times10^{-2}, 1.38\times10^{-1})$.

Application of the threshold test with $P^{*}=1.749\times10^{-1}$ results in the detection of airborne infections with a sensitivity and specificity of 82 and 94 per cent, respectively (see table 2 for details). Results are also shown for the detection of other infected premises including those where airborne transmission was considered unlikely and was ruled out. Predictions are plotted in figure 2, where farms suspected as having been infected have been plotted with filled (as opposed to open) circles.

The absence of uninfected premises data (but not infected premises data) beyond the locality does not affect the model fitting, since all suspected airborne transmissions occurred locally, but will have reduced the recorded specificity of results; conversely, the inclusion of non-local infected premises (had there been any classified as airborne infections) would have reduced the recorded sensitivity for detecting possible transmissions or unrelated infections.

In comparison, a model based not upon predicted virus emission and dispersion but purely upon proximity produces a test with a sensitivity and specificity of 64 and 62 per cent, respectively: to attain a sensitivity of 82 per cent (equivalent to the above model) would require a reduction of specificity to only 24 per cent in a distance-based model.

### *3.2. Surrey 2007 predictive model*

Parameter values obtained from fitting the model to the Hampshire 1968 outbreak were applied to emissions from all premises which could have been potential sources of infection—either by airborne transmission or otherwise—during the Surrey 2007 outbreak: the results are given in table 3. In most cases, suspected airborne transmissions are detected with a high level of specificity and sensitivity. For each of the four suspected airborne virus sources, the predicted risks of infection for all premises within the surveillance zone are plotted in figure 3.

In each case, the surrounding farms may be ranked according to their predicted risk of infection: this value is independent of the fitted parameters, although the actual level of risk is not. For each emission scenario, the rank of those farms that could have been infected by the given source premises is given in table 3: in most cases, only a small fraction of all farms in the surveillance zone would need to be checked in order for all infected premises to be detected, if the recommended order is observed. It is perhaps important to note that Surrey has a relatively low cattle density compared with other regions of the UK.

## 4. DISCUSSION

The prediction of airborne spread of virus has been successfully applied to FMD for considerable time (Gloster *et al.* 1981, 1982). Advances in meteorological modelling and data collection (Davies *et al.* 2005) have been accompanied by developments in emission profile and plume modelling (see, for example, Gloster *et al.* in press).

Given basic accurate information about a virus source, such as the number and species of infected animals and the time lesions that are likely to have first emerged, it is possible to produce a reliable virus emission profile (Gloster *et al.* in press) within an operational time scale. These data are usually available within a short time of a premises being suspected or identified as infected, following inspection. While the emitting species has a significant impact on the level and temporal distribution of emissions (Gloster *et al.* in press), recent analysis has suggested that at present there is evidence only for a small number of strains, which justifies deviation from a standardized emission profile (Gloster *et al.* in press); we note that changes in the magnitude of emissions alone would not affect the predictions made here, since this is equivalent to rescaling $\theta$ (while this would change the predicted risks $P_i(\hat{\theta})$, it would do so monotonically and thus be compensated for by the resultant change in the fitted value of the risk threshold $P^{*}$).

By making use of dispersion models driven by meteorological data from numerical weather prediction models or single-site observational data (Sørensen *et al.* 2000; Gloster *et al.* 2006), these profiles can be used to predict the spatio-temporal distribution of virus particles around a source or multiple sources, the output of which can be achieved in a matter of minutes or hours. It has been shown that these results can be easily applied to predict both the relative risk and, in

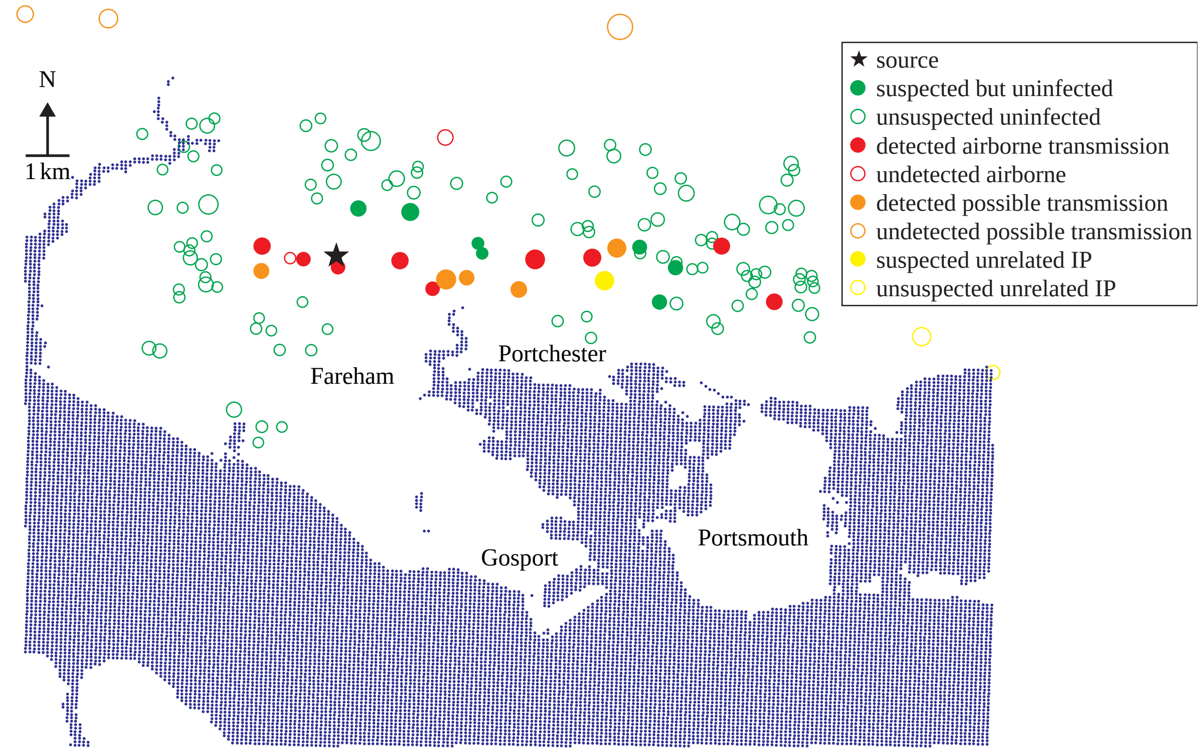

Figure 2. Location plot of all the recorded premises involved in, or close to, the 1968 Hampshire outbreak of foot and mouth. Circles are proportional to herd size, with colours related to the transmission routes (Sellers & Forman 1973) from an abattoir traced as the major source (star) of infection. Premises whose predicted risk of infection is over a threshold level are identified as suspicious (filled circles; green, suspected but infected; red, detected airborne transmission; orange, detected possible transmission; yellow, suspected unrelated infected premises), those below are not (open circles; green, unsuspected uninfected; red, undetected airborne; orange, undetected possible transmission; yellow, unsuspected unrelated infected premises). The outbreak occurred north of a large urban area on the coast: details of all infected premises associated with the outbreak were available, but only those uninfected premises local to the abattoir were recorded (see text for details).

Table 2. Results of applying the model to emissions from the abattoir in the Hampshire 1968 outbreak. (The sensitivity of the model as a predictive test is the proportion of infected premises successfully identified as above the critical risk threshold; the specificity of the test is the proportion of uninfected premises classified as not at risk. The model is only designed to identify airborne transmissions from the source specified: thus 2 out of 11 airborne infections were missed, while 7 out of 117 uninfected farms were incorrectly identified as having been infected. The detection of other transmission events is included (in italics) for interest only, in order to see what additional benefits this approach might have. The results for which the model was designed to give accurate predictions are shown in bold.)

| sensitivity | | | specificity |
|---|---|---|---|
| airborne route | *any route* | *all infected premises* | uninfected premises |
| successful detection of those infected premises classified (through tracing, etc.) as having been infected by the abattoir source through airborne transmission | *successful detection of any infected premises where airborne infection from the abattoir could not be excluded (including those where alternative routes were identified as more likely)* | *successful prediction of all infected premises, irrespective of the transmission route or source (including those involved in the outbreak but not associated with the abattoir)* | successful identification of all premises that remain uninfected |
| **9/11** | *14/20* | *15/25* | **110/117** |

specific cases, the absolute risk of airborne infection to local herds or flocks based upon their location and size.

Risk estimates do not perfectly predict subsequent events due to the inherent nature of stochastic events. For example, an analysis of the 2001 foot-and-mouth outbreak in the UK suggested that only 5–15% of infected premises were consistently identified with the use of transmission models due to the high level of variation between epidemics (Tildesley *et al.* 2008).

We believe, however, that the results here are an important proof of principle and that the data the model provides would be of genuine use during an outbreak. There is also value in analysing past events to help identify transmission pathways; in particular, the potential to prioritize for further investigation and contact tracing those premises that have been officially classified as having been infected by airborne transmission but where model predictions indicate

Table 3. Results of applying the model to airborne transmissions in the Surrey 2007 outbreak. (The risk rank of farms (the order for prioritizing inspection) is independent of any fitting, and a result of emission profiling and dispersion modelling only. Application of fitted values from the previous Hampshire 1968 outbreak provides a test for predicting airborne transmission: sensitivity and specificity relate to the successful classifications of farms as infected or not. The model is designed to detect airborne infection from the source premises: the detection of other transmission events is included (in italics) only to see whether additional benefits can be obtained through this approach but are not expected to be accurate. The results for which the model was designed to give accurate predictions are shown in bold.)

| source premises | premises possibly infected by the source subsequently, including their predicted risk of airborne infection (ranked out of all 258 other farms in surveillance zone) | | sensitivity (successful identification of infected premises) | | | specificity (successful identification of uninfected premises) |
|---|---|---|---|---|---|---|
| premises identified as the source of virus (table 1) | premises assumed infected by airborne transmission from the source | *premises possibly infected by airborne transmissions from the source but other route(s) identified* | premises assumed to be infected by airborne transmission from the source | *premises possibly infected by airborne transmissions from the source but other route(s) identified* | *all infected premises, including those where infection by the source considered impossible* | all uninfected premises within the 10 km surveillance zone |
| IP1b | IP2b (**4th**) IP2c (**6th**) | | **100% (2/2)** | *100% (2/2)* | *22% (2/9)* | **97% (241/249)** |
| IP2b | | *IP4b (52nd) IP5 (96th)* | | *0% (0/2)* | *11% (1/9)* | **92% (229/249)** |
| IP3b | IP6 (**73rd**) IP7 (**137th**) | *IP8 (46th)* | **0% (0/2)** | *0% (0/3)* | *22% (2/9)* | **88% (220/249)** |
| IP4b | IP3b (**34th**) | *IP3c (79th)* | **100% (1/1)** | *50% (1/2)* | *44% (4/9)* | **77% (192/249)** |
| IP6 | | *IP7 (28th) IP8 (1st)* | | *0% (0/2)* | *0% (0/9)* | **100% (249/249)** |
| IP7 | IP8 (**2nd**) | | **100% (*1/1*)** | *100% (1/1)* | *22% (2/9)* | **99% (246/249)** |

this as highly unlikely. This would be especially useful if combined with available molecular epidemiological evidence.

The model allows all herds or flocks of a given species surrounding an infection source to be quickly prioritized for inspection based only upon herd size and location (from which virus exposure is calculated): by constructing separate lists for each susceptible species results remain independent of the need for fitted parameters. In practice, every farm within the surveillance zone (at least 10 km around each infected premises) will be inspected and eventually tested. Thus, when there is a large number of false positives generated by a lower sensitivity test (e.g. 77%), this does not result in an actual increase in workload, but simply weakens the efficiency of predictions in helping to identify infected farms: in most cases, however, only a small fraction of farms would need to be checked in order to detect all infected farms (see rankings in table 3).

If results were to be used in isolation, false results could create more work by increasing the distances travelled by inspecting vets (as opposed to visiting farms by geographical area). We expect, however, that prediction be combined with other information, including the tracing of non-airborne transmission routes, and for a pragmatic approach to be taken in the field, e.g. by inspecting livestock very close to visited premises.

Explicitly quantifying the probability of airborne infection or to classify premises as suspect or not—as opposed to simply ranking farm risk—relies upon the model parameter $\theta$, which incorporates a number of properties and characteristics of both the virus and host species, so that these results are derived for the infection of cattle by O1 BSF1860 (Schley *et al.* 2008); suitable modification of emission profiles for other strains (see for example Gloster *et al.* in press), together with the data on strain-specific susceptibility of species would, however, allow results to be applied more widely.

Importantly, the fitting approach allows a number of strain- and species-specific factors (for which there are only limited, if any, data) to be modelled without their explicit inclusion. An alternative approach using parameter estimates (Cannon & Garner 1999), based on the experimental data (Donaldson *et al.* 1987; Martin *et al.* 1987), has been used with a similar modelling approach (Garner *et al.* 2006; Hess *et al.* 2008) to rank farms by risk and categorizing them into those at high, medium, low or very low risk: the prioritizing of farms for inspection is dependent only on the accumulated exposure dose and herd size, and is thus expected to be the same for both models; however, the categorization of risks uses arbitrary thresholds and may therefore not match with the test applied here.

In the absence of previous outbreak data for those strains considered to have significantly different dynamics and properties from those for which there are (current evidence of these is limited: see Gloster *et al.* in press), parameter estimates based on experimental results are required to generate predictions. The prioritization of animal groups for inspection, however, is independent of these parameters and could be very important in the control of any outbreak. Tildesley *et al.* (2006) considered the order in which emergency

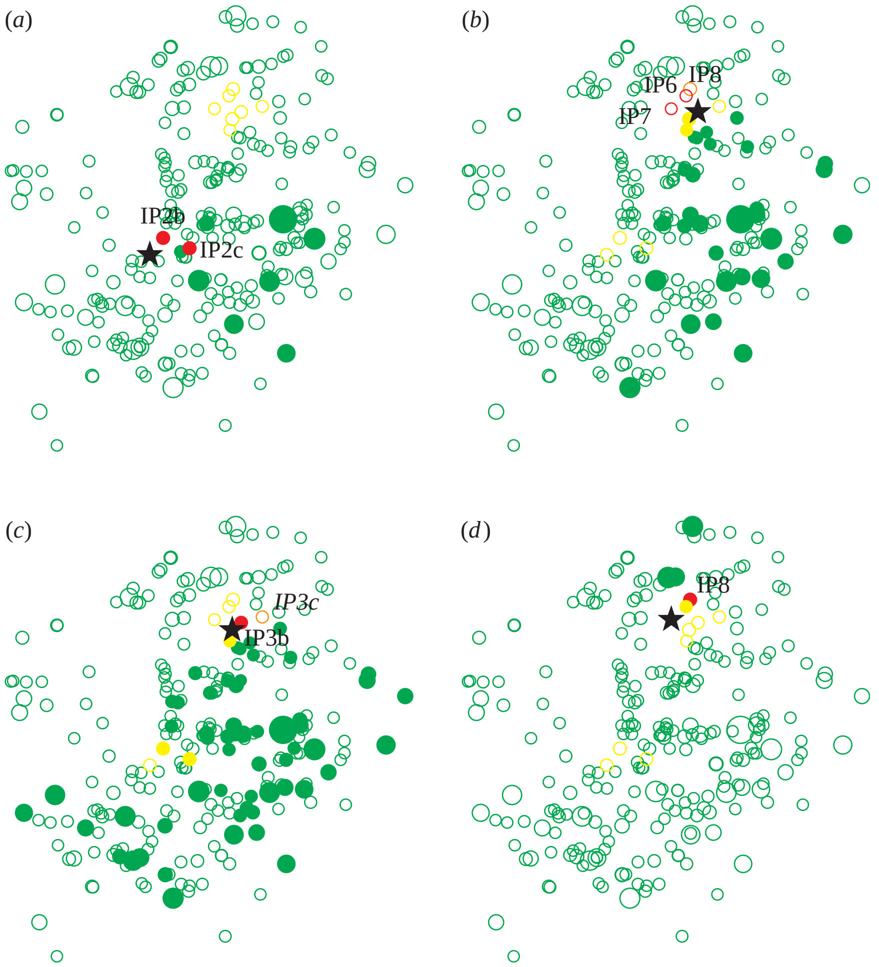

Figure 3. Relative location of all the cattle herds within 20 km of the primary site of the 2007 foot-and-mouth outbreak in Surrey, UK, plotted for each of the four suspected sources of airborne transmission (sources from which no airborne transmission was suspected are not shown: for results, see table 3). Key as in figure 2—with identifying labels for those IPs classified as probably or potentially infected via airborne transmission ((*a*) IP1b, (*b*) IP3b, (*c*) IP4b and (*d*) IP7). Predictions are based on the maximum-likelihood estimate and threshold value derived from the Hampshire 1968 outbreak: filled circles indicate those farms that should be prioritized for inspection.

vaccination should be carried out, based on farm type, and found that this had a significant impact on the overall size of an epidemic. Existing models using historically fitted transmission kernels (Keeling *et al.* 2001) have also been applied to determine the probability of undetected infection (Jewell & Roberts 2008). Because these apply the broad dynamics of an epidemic to approximate holdings data, i.e. using the Agricultural Census (2000 census by Tildesley *et al.* 2006; 2003 census by Jewell & Roberts 2008), however, these provide strategic rather than tactical information during an outbreak.

We conclude that, in addition to the efficient investigation and analysis of infected premises, successful prediction of airborne infection requires accurate animal location data. Unfortunately, the data currently available through either the UK Agricultural Survey (which does not provide a full census of ownership) or the Animal Movement Records maintained by all EU member states (which can only be obtained retrospectively) are not sufficient for this purpose, since information on animal location is, at best, limited to the address of the owner of the holding to which it is registered. The official report of the inquiry into the 2007 UK outbreak (Anderson 2008) includes a recommendation for a fully functional livestock data system. Results suggest that, if this included accurate animal locations, as opposed to holdings affiliation, this would be a valuable asset in future outbreaks of both FMD and other livestock diseases. The above results were only derived long after the outbreak had been established and the details of all livestock in the surveillance zone had been recorded; with an accurate database, however, predictions for a future outbreak could be made shortly following a source having been identified and inspected. Furthermore, a well-coordinated and reliable data system would allow for an automated or semi-automated process to be implemented through NAME, potentially allowing for the generation of advice on an operational time frame. Additional data on animal ages and housing, etc. could also be included in future models to increase the accuracy of predictions.

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