1. INTRODUCTION

Bovine tuberculosis (BTB) control in Great Britain (GB) cost over £90 million in 2005 including £35 million in compensation to cattle farmers (http://www.defra.gov.uk/animalh/tb/stats/expenditure.htm). Disease spread at the national level is due to both cattle movements and other causes. Particularly unwelcome is transmission from infected badgers, generally resulting in ‘high-risk’ areas that should be targeted to prevent further geographical spread of disease. With these areas expanding rapidly over the last decade, their close surveillance is important to both identify infected herds quickly, and limit their further growth.

Keywords: epidemic; Mycobacterium bovis; breakdown

Both badgers and livestock movements have been implicated in contributing to the ongoing epidemic of bovine tuberculosis (BTB) in British cattle. However, the relative contributions of these and other causes are not well quantified. We used cattle movement data to construct an individual (premises)-based model of BTB spread within Great Britain, accounting for spread due to recorded cattle movements and other causes. Outbreak data for 2004 were best explained by a model attributing 16% of herd infections directly to cattle movements, and a further 9% unexplained, potentially including spread from unrecorded movements. The best-fit model assumed low levels of cattle-to-cattle transmission. The remaining 75% of infection was attributed to local effects within specific high-risk areas. Annual and biennial testing is mandatory for herds deemed at high risk of infection, as is pre-movement testing from such herds. The herds identified as high risk in 2004 by our model are in broad agreement with those officially designated as such at that time. However, border areas at the edges of high-risk regions are different, suggesting possible areas that should be targeted to prevent further geographical spread of disease. As these areas expanding rapidly over the last decade, their close surveillance is important to both identify infected herds quickly, and limit their further growth.
between contiguous herds. Third, additional countrywide ‘background’ risk of breakdown through other causes is modelled, potentially accounting for unrecorded movements and contact with infected cattle occurring outside of high-risk areas. We consider two models for the high-risk areas, first based upon annual and biennial testing areas (i.e. parish-based or parochial high-risk areas), and second assuming a fitted radius of high-risk surrounding known BTB cases identified over 1 year (2003), to determine whether their spatial locations are good markers for the true extent of areas at high risk of BTB spread in the following year.

2. MATERIAL AND METHODS

We use cattle tracing system (CTS) data provided by RADAR (http://www.defra.gov.uk/animalh/diseases/vetsurveillance/radar/), details of BTB breakdowns reported to DEFRA’s animal health database, VetNet, and the June Agricultural Survey for 2003 (http://www.defra.gov.uk/esg/work.htm/publications/cs/farmstats_web/default.htm) as detailed in the electronic supplementary material. The movement data were consolidated into batches of cattle moved between pairs of georeferenced premises on given dates between 2002 and 2005 (see electronic supplementary material for georeferencing details). In brief, the model considered 130 755 locations, with 3 624 643 processed batch movements and contact with infected cattle occurring outside of high-risk areas. In the ‘low within-herd’ transmission model, μ only applies to those cattle that have previously passed through high-risk areas.

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The model is based upon a previously developed framework for modelling livestock disease transmission through movements and other mechanisms (Green et al. 2006; Kao et al. 2006). It operates at the level of the premises and is spatially explicit, using 1-day time steps. Breakdowns from 2003 in 1- and 2-year testing areas were used to set the initial state of the model (index cases). Premises at time \( t \) are infected with probability \( p_{ir} \). This probability is amended when the premises is exposed to infection through one of the three modelled routes (see electronic supplementary material for full details).

(a) Cattle movements

Cattle movements are a known BTB risk factor (Gilbert et al. 2005). Movements from infected premises are infectious with probability \( \mu \) per animal moved. We consider two possibilities: in the ‘high within-herd’ transmission model, all premises exposed to cattle that have been resident in high-risk areas are themselves a risk, so \( \mu \) applies to all cattle moving from exposed herds. In the ‘low within-herd’ transmission model, \( \mu \) only applies to those cattle that have previously passed through high-risk areas.

(b) High-risk areas

We assume areas with endemic BTB to be at higher risk of infection. Little is known of within-premises dynamics to distinguish among premises types; therefore, we assume all premises within specified high-risk areas as subject to infection with constant daily probability \( \gamma/n \), where \( n \) is the number of premises in high-risk areas. Two types of high-risk areas are defined: all premises in parishes with 1- or 2-year testing intervals (‘parochial’ high-risk areas); or all premises within a radius \( r \) of an index case.

(c) Background rate

All premises are subject to infection with a constant daily probability \( \beta \) to account for cases not explained by the other two factors.

Maximum-likelihood parameter estimates for \( \mu, \beta, \gamma, \) and \( r \) were obtained as described in the electronic supplementary material, with confidence limits provided by a Markov chain Monte Carlo algorithm.

3. RESULTS

The proportions of infections due to movements, background rate spread, and presence in high-risk areas, and with corresponding transmission rates \( \mu, \beta, \gamma \) and radius \( r \) are shown in table 1 and figure 1 (and figure A1 in the electronic supplementary material) for different modelling assumptions, using the year 2003 for model seeding, and the year 2004 for evaluation of the model likelihood function (given in the electronic supplementary material). Parameter \( m \), the assumed possible window of infection prior to discovery was set at 1 year, requiring a model start date at the beginning of 2002. Models were fit using a maximum-likelihood method and compared via the Akaike information criterion (AIC; Akaike 1974). Where models were nested (high within-herd versus low within-herd, background versus no background), statistical
significance was confirmed using likelihood ratio tests. The best-fit model assumed high-risk areas based on radii surrounding index cases, and low within-herd transmission, where only cattle that have stayed on premises in high-risk areas are assumed potentially infectious. Movement accounted for 16% of infections, with background infection 9%, and the remaining 75%, due to high-risk area transmission. The 95% CIs are narrow with confidence in the proportion of movement-related infections notably strong (figure 1). Model results were insensitive to the model start date and the infection window \( w \) (duration of infectiousness before reported breakdown) within the range of 70–365 days (figure A1 in the electronic supplementary material) due to repeated sampling from the high-risk areas (figure A2 in the electronic supplementary material).

VetNet data include both confirmed (via culturing of \( M. bovis \) or appearance of lesions typical of BTB) and unconfirmed cases. Including the unconfirmed cases in the analysis, the results (not shown) differed in an increased contribution of background spread of approximately 15%. The increase in ‘unexplainable’ breakdowns suggests that the majority of unconfirmed breakdowns are a low risk for onward transmission, either because they are inherently less infectious or more likely because they represent false-positive tests.

As a further test of model robustness, model fits were obtained with all time frames moved forwards 1 year, such that 2004 breakdowns were used to seed the model and the model output fitted against 2005 breakdown data, using the appropriate movement data. Results for the low within-herd transmission model were similar to those obtained for the 2003–2004 model fit, as shown in the electronic supplementary material (table A1 in the electronic supplementary material).

The model assumes that all premises included in the model are equally susceptible to infection given equal levels of exposure. As there are known risk factors (Gilbert et al. 2005), it is probable that breakdown farms are in some way more susceptible. To investigate this, breakdown herds were assumed inherently more susceptible than all other herds and the model refitted (figures A3 and A4 in the electronic supplementary material). This improved model fit, but did not substantially change the proportions of infection through the three routes (see electronic supplementary material), as all the risk factors increase proportionally.

The current control policy in GB requires annual or biennial herd testing and pre-movement testing in specified, high-risk parishes. Our results suggest that attribution of risk by areas centred on breakdown herds in 2003 would have identified 0.5% more of BTB-infected herds in 2004, reducing the infected herds not in these areas by 20% (table 2). This model has a lower AIC compared with models with parochial risk. However, since 1998, frequent testing areas have expanded dramatically in England and Wales (figure A5 in the electronic supplementary material), and the benefits of replacing the simply implemented parochial testing scheme with a more complicated approach would be small, if this is the measure used.

To test whether radial test areas perform better than parochial areas simply because they encompass more herds (figure 2), we replaced index cases with other premises selected randomly from the same parish, and compared radius-based high-risk areas centred on the breakdown herds with those centred on the randomized index cases. Similar parameters were thereby obtained, though model selection based on the AIC showed the models based on randomized cases to be substantially worse (table 1).
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movement-related infections).

Owing to the different time frames, and because our 

model includes all movement-based spread, formal 

comparisons with pre-movement testing data are not 

possible, however, in the first seven months of pre-

movement testing, 59 confirmed breakdowns were 

identified by the scheme. In addition, current policy 

requires pre-movement testing from certain premises not 

in 1- and 2-year testing areas are not considered infectious (an estimated 323 breakdowns, corresponding to 

93% of movement-related infections). This assumes no exemptions, and perfect testing of all cattle of all ages, but 
does not include cases accounted for under background rate spread. Using radius-based high-risk areas caused a 

greater reduction of 15.4% of breakdowns (98% of 

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4. DISCUSSION

The three modelled components encompass various 

routes of transmission. The high-risk area process could 
account for both direct farm-to-farm spread and spread 

from wildlife reservoirs. The background rate will include unrecorded movements, infectious movements that pre-
date those used by the model, and other long-distance transmission mechanisms such as fomites. It will also 
account for some overspill from high-risk areas. It does, however, make the implicit assumption that these 

processes occur at equal rate across the country. Little 

external data are available to quantify the proportions of 

these three ‘routes’ of transmission. In one earlier study (Wilesmith 1983; MAFF 1991), 89% could not be 

attributed to cattle movements. However, management 
practices will have changed considerably since this time. In 
contrast, badger removal in cull trials led to a decrease in 
confirmed incidence of only 19% compared with control 
areas (Donnelly et al. 2006), but was for several reasons an 

incomplete cull: it can only be seen as an estimated lower bound for breakdowns from a badger source.

Aside from the established links between BTB infection in badgers and cattle (Woodroffe et al. 2006), unrecorded movements of cattle and earlier movements (e.g. prior to 2002), contiguous grazing areas with infected cattle, and transmission due to human activities would all be expected to contribute to transmission in high-risk areas. However, they would also contribute similarly in areas of low risk provided infected herds in both high- and low-risk areas are otherwise similar. Where risk factors (e.g. grazing practices) are clustered, they will be represented mainly as part of the high-risk area spread. Under our assumption that the background process $\beta$ is similar in both high- and low-risk areas, transmission due to $\beta$ only accounts for 3% (54) of 

breakdowns in 2004 in high-risk areas. Outside of high-risk areas, background transmission accounts for 50% of 

breakdowns. This is consistent with a detailed investigation of a small cluster of breakdowns in northeast England (Gopal et al. 2006) where 16 out of 31 breakdowns contained at least one confirmed case traced from a 

breakdown herd with a matching molecular type of $M. bovis$.

Our model is fitted only to the observed epidemic and does not consider cattle harbouring $M. bovis$ but missed 
either through never having being tested or owing to test 

insensitivity (de la Rua-Domenech et al. 2006). However, 
in the absence of biases in these missing data, our estimate 
of the relatively low importance of cattle movements 
should be robust. It is also consistent with prior results 
showing that cattle testing alone can control cattle- 
to-cattle spread (Kao et al. 1997), and that few breakdown 
herds in low-risk areas contain infected homebred cattle 
(Gopal et al. 2006). Our model also assumes that BTB is a 
single homogeneous infectious agent across GB. This is a 
simplification: BTB exists in GB as numerous genotypes, 
most with a high degree of geographical clustering (Smith et al. 2006). Further work is required to determine the 
effect of incorporating such data into the model developed 
above, and whether there are identifiable inhomogeneities across the genotypes.

High-risk spread is probably the result of the cattle– 
badger–BTB interaction, though there is potential for contributions from other clustered risk factors. Evidence 
that cattle-to-badger transmission is important is sparse 
(Woodroffe et al. 2006), however if true, seedings via cattle 
infections may contribute to the broadening of high-risk 
areas (figure A5 in the electronic supplementary material).

Our model identifies significant areas that would not be 
under restriction given current protocols, suggesting that 
closer investigation is necessary for other areas not 
currently under restriction. While there appears to be 
little immediate benefit in terms of a reduction in herd 
breakdowns, other benefits of close surveillance must also 
be considered: close surveillance of high-risk areas will not 
only help to prevent spread to low-risk areas but it may 
also help to control the growth of the high-risk areas 
themselves.

Figure 2. Distributions of high-risk areas as estimated for 2004 (low within-herd spread model). Premises in both 

radius-based and parochial high-risk areas are shown in light grey, premises only in radius-based areas in dark grey, and 

only in parochial-based areas in black. Elsewhere is shown with a checked background.

The cumulative effect of transmission mechanisms is 

nonlinear, so to test the possible effect of control 

strategies, we selectively reduce each parameter to zero, 

rerun the model, and determine the effect on breakdown 

rate. Complete inactivation of all movement and back-
ground spread caused the maximal reduction of 24% 
simulated breakdowns in 2004. Selectively inactivating 

movement-related transmission alone in the best-fit model 

(low within-herd transmission) reduced the number of 
simulated herd breakdowns by 14.6% where movements 

from 1- and 2-year testing areas are not considered infectious (an estimated 323 breakdowns, corresponding to 

93% of movement-related infections). This assumes no exemptions, and perfect testing of all cattle of all ages, but 
does not include cases accounted for under background rate spread. Using radius-based high-risk areas caused a 

greater reduction of 15.4% of breakdowns (98% of 

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Owing to the different time frames, and because our 

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onward transmission further. We also reduce the rate 

parameter for high-risk area spread to zero. In the radial 

high-risk areas, this reduces simulated nationwide 2004 

incidence by 81%, including a 37% reduction in further 

spread onwards through movements.

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