Manipulation of contact network structure and the impact on foot-and-mouth disease transmission

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ABSTRACT

The movements of livestock between premises and markets can be characterised as a dynamic network where the structure of the network itself can critically impact the transmission dynamics of many infectious diseases. As evidenced by the 2001 foot-and-mouth disease (FMD) epidemic in the UK, this can involve transmission over large geographical distances and can result in major economic loss. One consequence of the FMD epidemic was the introduction of mandatory livestock movement restrictions: a 13-day standstill in Scotland for cattle and sheep after moving livestock onto a farm (allowing many exemptions) and a 6-day standstill for cattle and sheep in England and Wales (with minor exemptions, e.g. direct movements to slaughter). Such standstills are known to be effective but commercial considerations result in pressures to relax them. When contemplating legislative changes such as a change in length of movement restrictions we need to consider the consequent effect these could have on the emergent properties of the system, i.e. the network structure itself. In this study, we investigate how disease dynamics change when the local contact structure of the recorded livestock movement network in Scotland is altered through rewiring movements between premises. The network rewiring used here changes the structure of the recorded trade network through a combination of altered movement restrictions and redirection of movements between holdings and markets to avoid nonsensical activity (e.g. movements to markets on days when they are inactive) while conserving other characteristics (e.g. movement date as closely as possible and market sales of the correct animal production type). Rewiring results in networks with higher clustering coefficients and lower network density. The impact of rewiring on a hypothetical foot-and-mouth disease outbreak in Scotland was assessed by stochastic simulation, considering scenarios with and without exemptions to the standstill rules. As expected, rewiring leads to a decrease in outbreak size and - if standstill exemptions are prohibited – higher probability of smaller outbreaks. Without exemptions, a shorter movement standstill is almost as effective as a longer standstill period, indicating that a simpler biosecurity system would offer minimal additional risk for FMD. These results suggest that explicitly manipulating the contact network structure in a sensible way has the potential to significantly impact disease control.

1. Introduction

The movement of livestock between premises is known to play a critical role in the introduction and dissemination of infectious diseases among animal holdings. As evidenced by the 2001 foot-and-mouth disease (FMD) epidemic in Great Britain (GB), this can result in major economic loss (Haydon et al., 2004) and involve transmission over large geographical distances (Gibbens et al., 2001; Keeling et al., 2001). At the epidemic outset, FMD was predominantly disseminated by the rapid movement of sheep from Longtown market across the whole of GB. Following the end of the outbreak, mandatory livestock movement restrictions were introduced as a biosecurity measure (a 13-day standstill in Scotland for cattle and sheep after moving livestock onto an agricultural holding but with multiple exemptions[1] and a 6-day standstill cattle and sheep in England and Wales from 2003 with few exemptions) and the recording of livestock movements through livestock tracing

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systems became a legal requirement (Bourn, 2003; Vernon, 2011). The length of the respective movement regulations were chosen so as to be long enough for clinical signs of FMD to develop in infected animals, but minimises impact on livestock trading as market activities in GB often have a weekly tempo. Movement records can be used to accurately represent the dynamic connections between livestock holdings and markets, and they have become invaluable for identifying patterns critical to understanding the spread of any potential disease (Enright and Kao, 2016). An intuitive way of describing the structure of these contacts is as a *network*, where *nodes* represent premises and *links* between them are livestock movements (Dubé et al., 2009; Keeling and Eames, 2005; Martínez-López et al., 2009; Ortiz-Pelaez et al., 2006). Substantial heterogeneity has been observed in many livestock movement networks, often with a few individuals responsible for a disproportionately large number of contacts (Keeling and Eames, 2005; Shirley and Rushton, 2005). Thus targeting these highly connected individuals has the potential to be a highly efficient and effective way to control disease within the population (Christley et al., 2005; Kiss et al., 2006; Rautureau et al., 2012). However, targeting interventions at individuals who are selected on the basis of some network property, can also lead to network alteration where the structure of the network is explicitly changed and indeed network alteration is itself a potential disease control strategy. Here, we consider the potential impact of *network rewiring* (switching the destination(s) of edges) on FMD outbreak characteristics. First, we present a descriptive analysis of historical sheep and cattle movements taking place in Scotland within the 13-day standstill period for the years 2011 to 2013 to assess how movement regulations have influenced farmer behaviour, including the level of compliance with movement standstills. Then we outline our approach to using network analysis and adaptive network rewiring for epidemic control. We compare rewired networks to the recorded livestock movement network via standard static network measures such as average path length, density, and node-specific centrality measures. Finally, we summarise FMD simulations results on both the original record and on rewired dynamic networks, discuss their implications, and consider future research directions.

2. Materials and methods

2.1. Analysis of standstill compliance

Individual cattle and batched sheep movements between Scottish holdings from 01/01/2011 to 31/12/2013 were obtained from the cattle tracing system (CTS) and the Scottish Animal Movement System (SAMS). These datasets were pre-processed separately and subsequently combined for analysis. Under standstill regulations, movements from animal holdings direct to slaughter or to slaughter via a market are exempt from the 13-day standstill rule and were excluded from further analysis. Markets and slaughterhouses were identified through a list of sheep markets and slaughterhouses obtained from historical sheep movement data provided by the Scottish Animal Movement Unit (SAMU). Using the unique county-parish-holding (CPH) number as an identifier, the movement records were subsequently joined with the British Sheep and Goat Inventory to derive premises types, geo-referencing data, and numbers of animals held at each premises. Cattle movements are registered at the individual animal level and are reported both by the farmer at the holding of origin and the farmer at the holding of destination. After removing births and movements with identical destination and departure location, movement records were joined with location data to retrieve premises types. Movements that could be clearly attributed as being exempt from standstill regulations were excluded from the data.[2] Cattle production types were categorised

as described in Gates and Woolhouse (2015), whereas only a single category was used for sheep. Finally, the individual movement records were batched in order to calculate holding level standstill exemptions and combined with the batched sheep movements. Standstill periods were calculated as follows: for each unique destination premises we retrieved all subsequent movements leaving this particular holding and calculated the waiting time with respect to the earlier on-movement. Each movement falling into the standstill period (less than 13 days) but for which no exemptions were explicitly identified, were marked as movements breaking the standstill regulations.

2.2. Availability of data and materials

Due to the sensitive nature of the data used in this work, we are unable to make the data publically available. The data on sheep movements records retrieved from the Scottish Animal Movement System and the Agricultural Census are held by the Scottish Government, whereas the data on cattle movement records are held by the British Cattle Movement Service. All data are subject to data sharing agreements.

2.3. Network generation

We used recorded livestock movements to generate *rewired contact networks* by re-directing movements to markets (which could potentially carry higher risk), based on changes in farmer activity that are economically sensible and that could be theoretically implemented by adjusting the existing legislation. To investigate legislative changes in movement restrictions and market trade patterns, a *4-week period* (with an additional 2-week burn-in period) of recorded livestock movements was determined as sufficient. Rewiring was conducted under the assumption that individual movements will be conserved in number, volume, and as closely as possible in time. For example, if a farmer was not allowed to move a batch of livestock within Scotland on a given day, then he or she are assumed to move that same number of livestock in a single batch at the next acceptable opportunity. We generated 8 sets of movement networks based on a 4-week period of recorded sheep and cattle movements (October 2010) through the combinations of standstill length (6 or 13 days), standstill exemption (yes or no), and market-rewire (yes or no)). An adaptive algorithm was created to rewire the combined sheep and cattle livestock movement network by pushing movements violating a chosen standstill forward to the next legal date as closely as possible in time and by maintaining number and volume of the individual movements. The process was dynamic, with movements diverted to the next permissible date past the expiration of the standstill, and triggering a new standstill at the destination premises. Table 1 provides a descriptive summary of each scenario. To account for existing standstill exemptions, exempt movements were identified and removed during rewiring before applying structural changes to the livestock movement network. These movements were reinserted at the final stage of rewiring. Disallowed farm-to-market movements were pushed back to the next available market day of the same production type at the same market after the end of the movement restriction period, whereas farm-to-farm movements were delayed to the next legal day. Market movements for particular production types occur only on a limited number of dates during the calendar year, which can result in diverted movements occurring weeks or months after the recorded movement taking place. In order to account for this, movements were shifted to the market with nearest geographical proximity on the next available market day of the originally recorded production type, considering all markets in Scotland. Nearest markets

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[2] We aimed to identify "true" standstill violations by separating out movements associated with known exemptions and therefore allowed to move animals within the nominal

(footnote continued)

standstill period. Supplementary material A.2. summarises how standstill exemptions were treated for cattle and sheep movements in detail.

Table 1

Summary of rewiring scenarios. The total number of scenarios included each combination of possibilities (8 in total). The network name denotes the length of the standstill (e.g. 13 days), followed by information on whether the network was rewired to the nearest market (Rw +) or not (Rw-), and lastly whether standstill exemptions were allowed (Ex +), or prohibited (Ex-).

Name	Proportion of movements occurring on a different date from recorded	Number of movements	Proportion of departure farms affected by a diverted movement	Number of departure farms
6 days Rw- Ex-	0.185	51295	0.21	10487
6 days Rw- Ex+	0.059	52574	0.10	10554
6 days Rw+ Ex-	0.208	52353	0.23	10523
6 days Rw+ Ex+	0.067	52947	0.11	10564
13 days Rw- Ex-	0.247	45218	0.25	9930
13 days Rw- Ex+	0.083	50488	0.14	10474
13 days Rw+ Ex-	0.286	46937	0.27	9994
13 days Rw+ Ex+	0.096	51138	0.15	10496

were identified as follows: based on the geo-location data of the recorded market, a list of markets was generated in increasing order of distance from each of Scotland's 891 agricultural parishes. This could then be applied to market movements during the rewiring process.

2.4. Network measures

Network measures (Wasserman and Faust, 1994) can be used to gain information about the dynamics of disease spread through analysing the network contact structure (Dubé et al., 2011a; Kao et al., 2006; Kiss et al., 2006). In this section, we give a brief overview of the network measures that we used to investigate the livestock movement networks and on which we conducted FMD outbreak simulations. All of the monthly networks were analysed by including the direction of the links, i.e. as directed networks.[3] On the whole, the rewiring process leads to different contact structures that can be represented by networks and examined with network measurements. While the network is dynamic, static network measures have been shown to provide useful information on the relative risks associated with the GB livestock network (e.g. Kao et al., 2007). The static network measures applied here can be broken down into network-level measures (global network measure) and node-level measures. There are many node-level measures that can be used to assess the importance of individual livestock holdings in the livestock movement networks. Among those are *betweenness* and *degree*, which allow for the identification of the centrality of individual nodes, and as a result their potential importance to disease propagation within the livestock movement network. The betweenness of a node represents the frequency with which a livestock holding is in the shortest path between pairs of nodes in the network, whereas a node's degree represents the number of direct contacts per holding (Freeman, 1978). Premises that have many contacts and are therefore at the centre of activity are often referred to as *hubs*. In terms of disease spread, identifying both high-degree and high-betweenness nodes can be useful as high-degree nodes are likely to become infected early on in an epidemic and high-betweenness nodes are likely to accelerate the spread of infection through the network. Similarly, targeting these key actors for rapid disease control can be extremely effective (Keeling et al., 2011). In a directed network where we consider the direction of trade, both the number of incoming connections (*in-degree*) and the number of outgoing connections (*out-degree*) can be considered (Wasserman and Faust, 1994). Global network measures on the other hand can be used to assess how connected the network is as a whole. Besides the node-level centrality measures described above, six network-level measurements (density, degree assortativity, average path length, diameter, density, connected components (strongly / weakly connected components)) were calculated for each monthly network

using R (version 3.2.1) (R Developement Core Team, 2015) and the R package igraph (Csárdi and Nepusz, 2006).

The *density* of a network indicates how connected the nodes are and is defined as the proportion of links among livestock operations in the network that are currently observed (see Dubé et al., 2009; Wasserman and Faust, 1994). A value of one implies that all potential connections are realized. The *diameter* of the network is the largest shortest path in the network. The bigger the diameter of a network, the less connected a network tends to be. For livestock movement networks, *degree assortativity* describes the tendency of a holding to be preferably connected to holdings which have degrees similar to their own (degree assortativity close to 1). In networks with disassortative mixing, high-degree holdings tend to be connected to holdings with a low degree and vice versa (degree assortativity close to −1) (Newman, 2010). Generally speaking, the maximal outbreak size of an epidemic is driven by the *component* structure of the network where components represent subgroups of nodes in which all pairs of nodes (i.e. livestock holdings and markets) are directly or indirectly connected. Networks are not necessarily connected and not every node is reachable from all others, however many real-world networks exhibit a giant component that contains the majority of nodes in the network. How connected a network is typically determines how fast and far a disease can spread. Connected components can be described as subnetworks within a network and can be divided into strong connected components and weak connected components. In essence, weakly connected components represent subnetworks for which a path exists between any pair of nodes, irrespective of the link direction. Likewise, strongly connected components are subnetworks where each network node can be reached from every other node in the network through either one or multiple directed paths. Importantly, if a disease enters a holding within a strongly connected component it can potentially reach any other holding within that strong connected component. It has been suggested that identifying strong components of a network is vital in estimating the population at risk of infection because introduction of disease into a node within the strong component puts all other nodes within that component at risk (Kao et al., 2006; Kiss et al., 2006). In animal movement networks, the calculation of a giant strongly connected component (GSCC) size may then be used to estimate potential epidemic sizes. In a livestock movement network the *average path length* represents the shortest path among two livestock holdings averaged over all existing pairs of holdings in the network (Dubé et al., 2011a,b, 2009). The *clustering coefficient* measures the degree of interconnection which may exist between neighbours of a node of interest (Watts and Strogatz, 1998), where a high degree of clustering can reduce the size of an epidemic (Kiss et al., 2006).

2.5. FMD simulation model

We developed a spatial stochastic model of FMD transmission and control (adapted from Green et al. (2006)) to investigate the impact of

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[3] Note that we use the terms nodes and links when we refer to networks generally, but use the terms holdings / premises and movements when discussing implications specific for the contacts considered in the study.

changed standstill regulations and of structural changes to the livestock movement network through a combinations of:

(i) two different movement restriction regimes (by applying either a 13-day standstill or 6-day standstills after livestock are moved onto an agricultural holding),
(ii) two different rewiring regimes (re-directing movements to the nearest market of the same production type or not),
(iii) two different exemption regimes (either exemptions to the standstill regulations were allowed or there were no exemptions).

The simulation framework combined dissemination of FMD through direct farm-to-farm movements, via movements through markets, and via local spread, along with control measures that included examination of dangerous contacts and culling of animals on confirmed premises. The model was individual-based at the level of the holding, and generated infection stochastically while replaying recorded livestock movements. Livestock movements and events of local spread occur on specific dates and based on these timings, each farm could be classified into one of five compartmental states:

(i) S – these are holdings with susceptible animals only.
(ii) H – these are restricted farms, i.e. farms that have exposed animals on them, but these animals are subject to isolation until the end of the movement restriction period (prompted by the movement of animals onto the farm). Here, the length of the movement restriction period is dependent on the chosen standstill scenario, taking on either 6 days or 13 days. There is not yet risk for transmission to other farms, neither by movements nor by local spread.
(iii) E – farms that can infect other farms by moving exposed animals only, not by local spread. A latent (incubation) period of five days was used.
(iv) I – farms with infectious animals (after the incubation period). These farms are a possible source of infection (either by off-movement or local spread).
(v) R – farms that are either culled or under control, thus do not cause a risk of further infection.

To allow for the dissemination of the pathogen, the infection was seeded at five farms that are known to have moved sheep onwards within three days after the start of the simulation. Seed cases were put into the I (infectious) compartment, and the disease was allowed to spread unrestrictedly for 20 days, which is broadly similar to the period for which FMD remained undetected in Scotland at the beginning of the 2001 UK outbreak (Gibbens et al., 2001). After this a national movement ban is imposed so that infections can only spread locally. As markets do not permanently keep livestock, they become disinfected and re-enter the S state at the end of the day after any off-movement. The simulation finished when there were no infected ($E, H,$ or I) farms in the population.

2.5.1. Infection through animal movements

Disease spread through direct farm-to-farm movements was implemented as outlined in Green et al. (2006), where the probability of farm infection through a movement of batched animals of size b with at least one infected animal was set to $1-(1-\mu)^b$, with each animal infected with probability μ set to 0.02.

To calculate the probability of a farm to become infected by a transitional on-movement of livestock, i.e. livestock that was sold through a market, several adaptions where made to the Green et al. (2006) model - the main difference being that the model makes use of the knowledge whether movements originated from an infected premise (IP): (i) It was assumed that farms in the H compartment (i.e. farms with dedicated isolation facilities) could not get infected locally as the farm had been infected through livestock movements and hence

will already host infectious animals (local infection will take longer to develop). These farms were not yet infectious by local spread (due to the on-farm restrictions) but could infect other farms locally after the incubation period had passed (an incubation period of 5 days was used). (ii) Where information about the source farm of moved livestock was unavailable, the probability that a batch of livestock containing at least one infected animal which can transmit an infection onto a farm was set to $p_{trans} = 1 - (1-\mu)^b$ (μ is assumed to be the same for batched livestock sold on the same day). (iii) Whenever the movement recording system allowed the identification and tracking of batched livestock, the probability of transmission was corrected to account for a higher infection probability for livestock originating from an infected farm than for livestock originating from a susceptible farm. This was implemented by adjusting the new probability of transmission to $p_{trans} = 1 - (1 - \mu_F)^i (1 - \mu')^s$, where i is the number of animals moved from infected farms, s is the number of animals moved from susceptible farms, μ_F is the probability of infection through a known movement from an infected farm for one animal (which is higher than μ), and μ' *is the* probability of infection from susceptible farms. Hence, the increase of infection probability of livestock sold from an IP was counterbalanced by a decreased probability of infection from susceptible farms (μ'), which relates to a baseline risk of infection due to contact with infectious animals from other batches at the market. To ensure consistency with the earlier model, μ_F was set to 0.02, μ was chosen to be the same as for off-market movements (0.004), and μ' was fitted so that the overall force of infection via markets for each market was the same as estimated in Green et al. (2006) (i.e. the average number of infected premises generated by one market through transitional passage of sheep which originated from an IP).

2.5.2. Infection through local spread

Infection through local spread was modelled using the same constant rate of generation of new cases as applied in Green et al. (2006), with a β-value of 0.065 per day on the infectious holding. This β-value has been proven to reproduce similar epidemic peak numbers (both for local spread and spread through movements) as observed in the 2001 FMD epidemic in the UK (Gibbens et al. 2001). On each simulation day, a number of infectious contacts were sampled from a Poisson distribution without replacement, independently for each infectious farm. Only farms that were known to keep livestock (as retrieved from the agricultural census) were considered for this. Infectious contacts were then chosen from all susceptible farms using a radius of 10 km and weighted in proportion to the distance d by $p \sim e^{-ad}$, where a was specified as $a = 0.5 \, \text{km}^{-1}$.

2.5.3. Control strategies (C)

Control programmes are often complicated and can range from preemptive culling to vaccination of 'at risk' animals. In this framework, we simulated control measures using two mechanisms: (i) detection of infectious premises after a certain number of days with clinical signs and (ii) contact tracing of on- and off-movements to target serological examinations at farms that could have received infected animals. The model assumes that after 7 days of clinical signs a farm would be reported to be infectious by the owner, which then would lead to diagnosis and removal (i.e. culled or put under restrictions that will allow for no further spread of infection). Contact tracing was implemented iteratively, starting with the first confirmed case. Once a farm was confirmed to be an IP, all animals kept on the farm would be culled within 24 h. Subsequently dangerous contacts (DC) have to be identified and farms that are at risk of infection need to be examined. It was assumed that there would be no pre-emptive culling, only diagnosed farms would be removed. Confirmed IPs were transferred to the (R) compartment and could not infect other farms. To obtain farms that traded livestock with an IP, the contact tracing window was set to 21 days, which is in agreement with current policies in the UK. During the simulations we obtained all on- and off-movements for the IP that
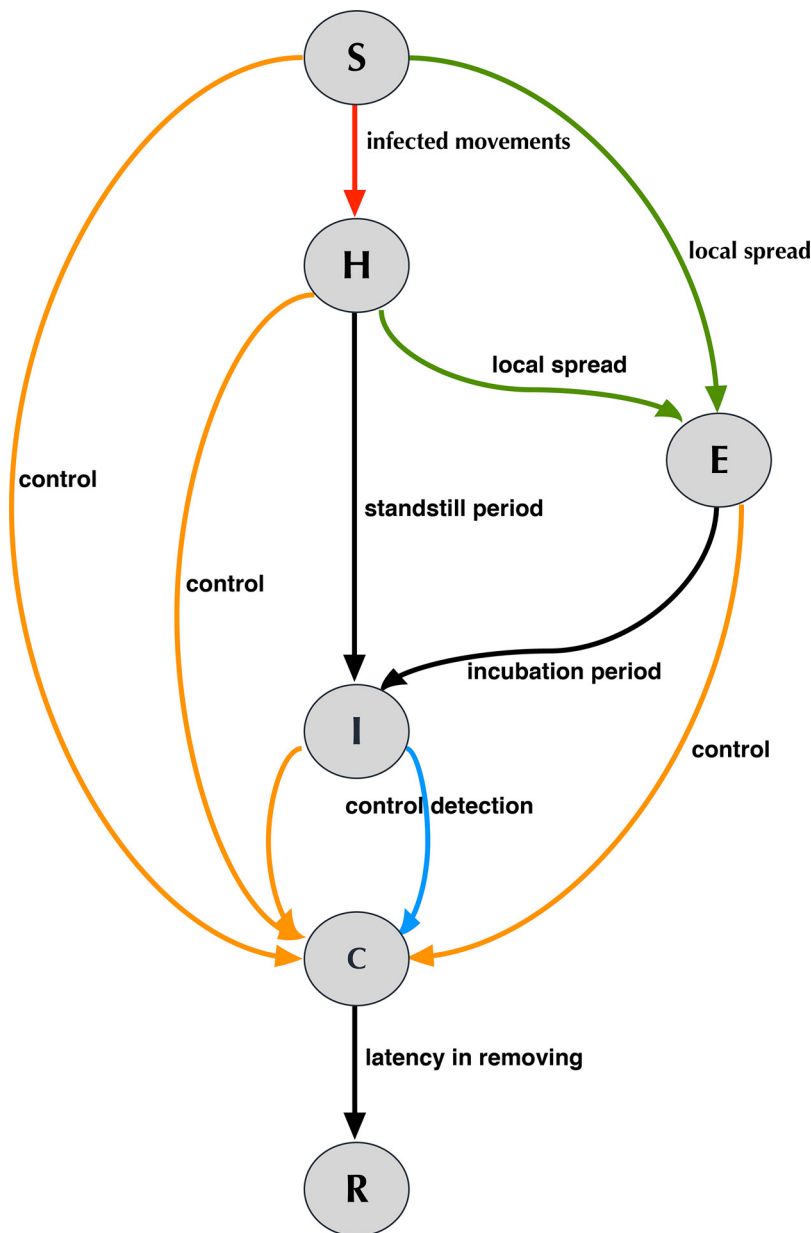
Fig. 1. The transition diagram of the model. Susceptible farms (S) can get infected via local spread (E) or infected animal movements (H), and then become infectious (I) after a certain period of time. Susceptible or infected farms can be removed (culled or taken under control) by moving through the (C) compartment to (R). Farms with clinical signs in animals (I) can be detected during examination or contact tracing. Farms that were confirmed to be infected are placed into the confirmed compartment (C) and will then be moved to the removed compartment (R) within a short period of time. Only farms from (I) and (H) (after having passed the incubation period) can infect others.

occurred within 21 days preceding the identification and: (i) direct contacts were transferred to the investigation queue and examined after 1 day (to simulate latency in contact tracing) (ii) for movements through markets, dangerous markets (i.e. those receiving or sending animals to or from the IP) were identified and all recipients of animals on those days were transferred to the investigation queue and examined after 4 days. Contact tracing procedures were performed iteratively, starting with farms that were diagnosed by clinical signs first. Once the examined farm was confirmed to be infectious, it acquired IP-status and the same procedures were performed for its contacts. For farms that were not infectious, no further contact tracing was triggered. The transition diagram of the compartmental model including control measures is visually summarised in Fig. 1.

2.5.4. Epidemic simulations

Simulations were set to start at 20 randomly selected dates throughout the specified month and this process was replicated at the beginning of each simulation to introduce additional stochastic variation (the parameters used in the model are summarised in Supplementary Material, Table A.3). A total of 1000 simulations were performed for the recorded movement network and the alternate re-wired networks. We quantified distributions of epidemic size using the Harrell–Davis estimate of the deciles (Wilcox, 2012). The 95% percentile bootstrap confidence intervals were computed from 1000 samples. To quantify differences between deciles of epidemic size distributions, we used the shift function, which is a robust statistical tool that allows to compare whole distributions by assessing if and to which extent two distributions differ (Doksum, 1977; Rousselet et al., 2017; Wilcox, 2006, 1995).

3. Results

3.1. Descriptive summary of standstill compliance

As a first step, we reviewed three years (2011–2013) of recorded sheep and cattle movements in Scotland under the existing standstill rules of 13 days regarding how these regulations have influenced farmer behaviour, and in particular their level of compliance with them. For 19,924 unique sheep holdings in Scotland (including markets) we retrieved 193,792 batched movements and calculated their
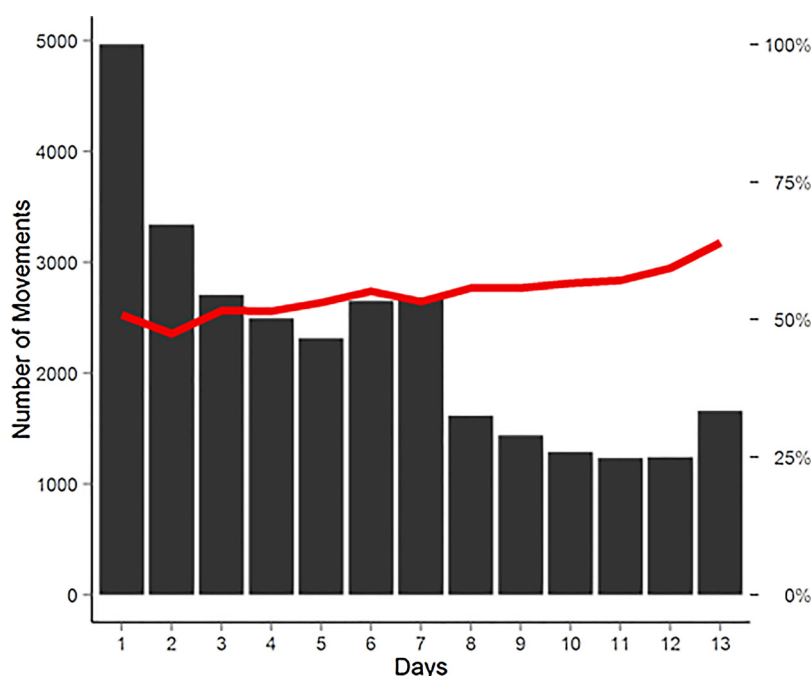
Fig. 2. Frequency of combined sheep and cattle movements (2011–2013) during the standstill period, aggregated by waiting time after standstill regulations take effect. The red line indicates the proportion of movements that appear exempt (as reflected by the percentage scale on the right) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

corresponding standstills periods. There were 39,686 movements from 4584 unique sheep holdings in total that fell into the 13-day standstill period. A total of 18,925 movements within the 13-day standstill period are exempt and allowed to move animals within that period (47% of movements within the standstill period). There were 20,761 that were identified as movements potentially breaching standstill regulations (10% of the total number of movements). For the cattle movements, we counted in total of 20,990 movements from 9723 unique cattle holdings in Scotland that fall into the standstill period. Of these, 10,026 movements occurred within 13 days and are considered exempt (47% of movements within the standstill period) while 10,964 movements violated the standstill rule.

Fig. 2 shows the number of combined cattle and sheep movements after excluding identifiable exemptions. The number of movements were aggregated by waiting time and plotted for the standstill period of 13 days after a movement ban had been taken effect. The red line indicates the proportion of movements that appear exempt (as reflected by the percentage scale on the right). As can be seen from Fig. 2, most animals are moved on day 1 after the movement ban had been imposed. As on-movements of one species can impose a standstill on another species, it is important to identify mixed species holdings. This was done by matching the list of actively trading sheep holdings against cattle holdings for the study period in question, with 77% of cattle holdings (7488 of 9723) recording movements found to be also actively trading sheep. There are twice as many mixed holdings with authorised separation agreements[4] than single species holdings (see Tables 2 and 3).

Nevertheless, single species holdings are more likely than mixed species holdings to have a recorded agreement (Relative risk = 1.26; 95% CI: 1.24,1.29). Mixed holdings appear to predominantly rear beef (see Table 3). Comparing exempt versus non-exempt movements according to their destination type (animal holdings, landless keepers, or

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[4] Holdings with separation facilities, where livestock brought onto a farm can be kept away from other livestock within the business while movement restrictions are in place, can apply for a livestock separation agreement to be put in place with the Rural Payments and Inspections Division's (RPID). With the RPID's approval, these businesses can avoid a 13-day standstill across the entire holding, given that animals brought onto the holding are kept separate from other animals on the farm, and the 13-day standstill will apply only to the livestock that was brought on, and not to other animals on the farm.

Table 2
Comparison of cattle only holdings to mixed holdings (sheep & cattle) with authorised separation agreements (top row) and without agreement (bottom row).

	Cattle Only	Cattle & Sheep
Agreement	2083	5674
No Agreement	152	1814

Table 3
Count of herd types for mixed holdings (sheep and cattle) compared to count of herd types for cattle-only holdings.

	Beef	Dairy	Mixed	Other
Cattle only	2134	339	19	9
Cattle & Sheep	7749	1249	69	22

Table 4
Number of movements within the 13-day standstill period, separated by species type and grouped by location type. For each species, the top row denotes movement that are exempt, the bottom row denotes standstill violations. There is no significant different between exempt and non-exempt movements according to destination type.
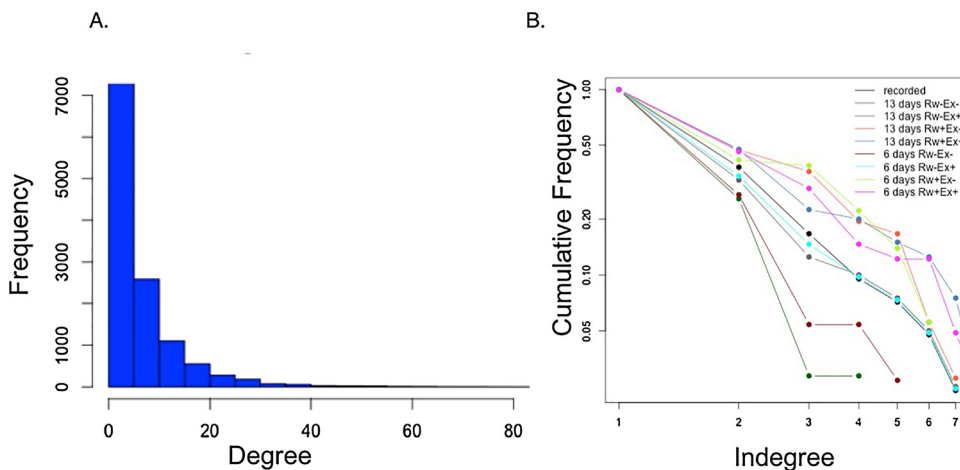
Species	Status	Animal Holdings	Landless Keepers	Markets
Cattle	Exempt	4173	129	5724
	Not Exempt	3967	136	6861
Sheep	Exempt	18889	14	22
	Not Exempt	20624	23	114

markets), there are no significant differences between the destination location type for movements within 13 days). For cattle, non-exempt movements are more often to market than exempt movements, although the difference is small (see Table 4).

3.2. Network analysis

The networks were aggregated on a monthly scale, analysed separately and then compared. The contact distribution for the 'baseline'

A.

B.

Fig. 3. A. Long-tailed degree distribution for the recorded movement network on original scale. B. The distribution of in-degrees of markets only in the cattle / sheep network considering all nine scenarios, plotted on a log-scale. Names for each scenario were chosen so that the number at the beginning of each name represent the length of the standstill period applied to the respective scenario, followed by whether it had been rewired to the nearest market or not as indicated by binary categories (Rw+ / Rw-), and finally whether standstill exemptions were allowed or not (Ex+ / Ex-).

network (the originally recorded cattle and sheep movement networks) exhibits a highly right skewed pattern where a small number of individuals ("hubs") make a disproportionately large number of contacts. These hubs establish many outgoing links and are influential on how far and fast a disease can spread within the population (Keeling and Eames, 2005; Kiss et al., 2006; Volkova et al., 2010). The rewiring technique applied in this analysis does not have a meaningful effect on the overall contact distribution[5] (Fig. 3A). However, as movements to markets are re-routed, the ingoing contact structure of markets is affected (Fig. 3B). This is related to the fact that most movements violating movement restrictions are movements between animal holdings, not transitional movements via markets (~74% of non-exempt movements are direct farm-to-farm movements). Hence, this did not lead to a systematic increase of the median indegree.

Livestock contact networks have been shown to exhibit small-world properties such as the local clustering of contacts with the occasional long-distance jumps that allows for spreading disease to more distant network communities (e.g Kao et al., 2006; Watts and Strogatz, 1998). Table 5 summarises the global graph properties for each of the rewired scenarios and the observed livestock movement network separately. As can be seen in Table 5 the degree assortativity coefficients (or Pearson correlation coefficients (r)) of all networks exhibit disassortative mixing ($r < 0$). This implies that dissimilar nodes tend to connect to each other and hubs are unlikely to connect to other hubs (Kao et al., 2006). The originally recorded network exhibits small-world properties, which is reflected in short average path length compared to a random network of similar size. Rewiring significantly increases both the average path length and diameter for all rewired scenarios compared to the recorded livestock movement network. This has important implications for FMD transmission dynamics in the pre-movement ban phase: potential disease pathways are reduced and distant communities therefore less likely to be affected (Gibbens et al., 2001; Keeling et al., 2001). As illustrated in Table 5, the size of the GSCC (36% of the overall network) and GWCC (100%) of the recorded movement network are reduced through re-routing the existing links. The diameter of each rewired network increases substantially because rewiring leads to one isolated component within the GSCC. All artificially generated networks resulted in networks with higher clustering coefficients, and lower density for the artificially generated networks compared to the recorded movement network.

In Table 6, we report measures that are indicators of network connectivity ("centrality measures") for the giant strong connected component for each rewired network grouped by premises type (animal holdings (AH) or markets (MA)). Unsurprisingly, markets are *hubs* in

the livestock movement network as reflected in the large number of connections they make (the *degree*) and the amount of control that these market nodes exert over the interactions of other nodes in the livestock movement network (i.e. their *betweenness*). The overall degree does not meaningfully change between the rewired scenarios compared to the originally recorded movements. For markets, their average betweenness increases through any chosen manner of rewiring. However, the number of incoming connections (*indegree*) of markets does not systematically increase as this is depended on (i) the presence of standstill exemption (i.e. animals moved from any of the Scottish Island areas to markets on the mainland are currently exempt) and that (ii) non-exempt movements which are pushed forward are mostly movements between animal holdings (~74% of non-exempt movements).

3.3. Epidemic size

All rewiring scenarios lead to a decrease in final epidemic size compared to the simulated FMD outbreak on the recorded movements (see Table 7).

The presence of standstill exemptions irrespective of the length of the standstill period on average increases the probability of a larger epidemic. A simulated FMD epidemic in these scenarios result in larger number of infections than the FMD simulation where absent and epidemic size tended to be smaller.

Given that we were interested in assessing the risk and benefits of a potential change in movement standstill policy towards a shorter standstill period of 6-days, in further analyses we focus on only four FMD simulation scenarios: (i) the "extreme" scenario with a 13-day standstill and no allowed exemptions ("13 days Rw- Ex-"), which should reflect the "best" simulation outcome compared to the FMD simulation on the empirical observed movements in terms of a reduction in total number of infections, (ii) a scenario which mimics the England-Wales standstills approach, i.e. a 6-day standstill with a much reduced number of exemptions ("6 days Rw+ Ex-"), (iii) and the FMD simulation output on the recorded movements ("Recorded") as a baseline to which we compare the rewired scenarios to. While the 'best' scenario is highly unlikely to be implemented by the livestock industry as it is associated with significant economic cost, the 6-day-, no-exemption-scenario is similar to the one implemented by England and Wales, and may offer a feasible alternative to the current regulations in Scotland.

Visually inspecting the distributions of epidemic size in Fig. 4 suggests that both rewired scenarios significantly differ from the simulated outbreak on the recorded movements, with the FMD simulations on the recorded movement scenario more likely to result in much larger outbreak numbers. A bootstrapped Kolmogorov-Smirnov test (1000 samples) confirms significantly ($p < 0.001$) smaller outbreaks on the rewired networks. Interestingly, despite being substantially more

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[5] Note that we used network measures as a tool to compare model output differences and our results should not be interpreted as denoting real contact networks.

Table 5
Summary of global graph properties for the rewired network and the observed network (bottom). The network name denotes the length of the standstill (e.g. 13 days), followed by information on whether the network was rewired to the nearest market (Rw +) or not (Rw-), and lastly whether standstill exemptions were allowed (Ex +), or prohibited (Ex-).

Network	Size (No. of nodes)	Edge count	Avg.path. length	Dia-meter	Density	Clust. Coefficient	Assortativity	GSCC	GWCC
Recorded (13days standstill	14,608	76,691	2.9	7	5×10^{-4}	6×10^{-3}	−0.118	5,290 (36%)	14,608 (100%)
13 days Rw- Ex-	14,396	59,508	4.3	12	3×10^{-4}	1.4×10^{-2}	−0.160	3,449 (23%)	13,833 (96%)
13 days Rw- Ex +	14,526	65,240	4.1	12	3×10^{-4}	1.5×10^{-2}	−0.153	4,291 (29%)	13,997 (96%)
13 days Rw + Ex-	14,432	65,241	3.8	11	3×10^{-4}	1.3×10^{-2}	−0.180	3,611 (25%)	13,876 (96%)
13 days Rw + Ex +	14,546	67,712	3.9	11	3×10^{-4}	1.5×10^{-2}	−0.161	4,355 (29%)	14,020 (96%)
6 days Rw- Ex-	14,655	66,032	4.1	12	3×10^{-4}	1.5×10^{-2}	−0.156	4,380 (29%)	14,129 (97%)
6 days Rw- Ex +	14,612	67,242	4.1	12	3×10^{-4}	1.6×10^{-2}	−0.154	4,539 (31%)	14,088 (96%)
6 days Rw + Ex-	14,651	70,600	3.8	11	3×10^{-4}	1.5×10^{-2}	−0.169	4,446 (30%)	14,122 (96%)
6 days Rw + Ex +	14,625	68,997	3.9	12	3×10^{-4}	$1.6 \ 10^{-2}$	−0.159	4,561 (31%)	14,103 (96%)

Table 6
Network summary statistics for recorded and rewired network reporting indegree, outdegree, degree, and normalised betweenness grouped by type (Markets (MA) vs. Animal Holdings (AH)). The network name denotes the length of the standstill (e.g. 13 days), followed by information on whether the network was rewired to the nearest market (Rw +) or not (Rw-), and lastly whether standstill exemptions were allowed (Ex +), or prohibited (Ex-).

Network	Type	Degree median	In-degree median	Out-degree median	Betweenness median	Out-degree min	Degree max.	In-degree max.	Out-degree max.	Betweenness max.
Recorded	AH	7	3	3	1.25E-05	1	655	652	103	0.015
	MA	244	112	106	0.01	5	1796	768	1028	0.129
13 days Rw- Ex-	AH	5	2	2	6.28E-05	1	52	21	49	0.026
	MA	217	89	89	0.04	1	1189	525	664	0.346
13 days Rw- Ex +	AH	6	3	3	4.91E-05	1	290	278	94	0.048
	MA	232	100	95	0.03	1	1648	699	949	0.341
13 days Rw + Ex-	AH	5	2	2	8.56E-05	1	80	25	74	0.012
	MA	191	87.5	92	0.03	1	1440	645	795	0.308
13 days Rw + Ex +	AH	6	3	3	5.41E-05	1	291	279	95	0.033
	MA	247	110	104	0.02	3	1778	773	1005	0.352
6 days Rw- Ex-	AH	6	3	2	5.59E-05	1	80	66	74	0.023
	MA	240	100	107	0.027	1	1634	696	938	0.343
6 days Rw- Ex +	AH	6	3	3	4.60E-05	1	294	282	98	0.044
	MA	238	104	91	0.025	3	1693	718	975	0.333
6 days Rw + Ex-	AH	6	3	2	6.21E-05	1	127	73	94	0.009
	MA	298	108	153	0.02	3	1940	813	1127	0.325
6 days Rw + Ex +	AH	7	3	3	4.90E-05	1	294	282	98	0.035
	MA	254	105	103	0.02	2	1798	790	1008	0.327

restrictive, the extreme scenario where no standstill exemptions exist does not provide substantially greater protection compared to the 'England-Wales' scenario.

To assess in what respect the 'England-Wales' scenario differs from the 'extreme' scenario, we used the shift function (Rousselet et al., 2017), As Fig. 5 illustrates, the two rewired scenarios only differ in the right tail, which is captured by significant differences for deciles 6 to 9 (Fig. 5.B).

3.4. FMD model simulations: spatial effects

In order to determine if the impact of legislation changes varied regionally, we generated spatial maps of the FMD model output for each rewired scenario and compared them to the spatial maps for FMD simulation outputs on the originally recorded movements. The number of infections per $10 \, \text{km}^2$ grid square were counted and averaged over 1000 simulation runs, and compared at each grid square to the outputs of each rewired scenario. Fig. 6 (left) shows the number of infections per $10 \, \text{km}^2$ grid square for the FMD simulation on the recorded movements. As expected, both rewired scenarios result in a smaller number of infections per $10 \, \text{km}^2$ grid square than compared to a simulated FMD outbreak on the recorded movements, with similar geographical distributions of reductions (though with the 13-days Rw- Ex- scenarios showing broader benefit).

4. Discussion

Scrutinising potential legislative changes for the trade network in Scotland requires that we not only take into account how this affects individual decision-making but also how this might alter the emergent properties of the network structure itself. In this paper, we investigated how changing the local contact structure simultaneously through

Table 7

Descriptive summary statistics of FMD simulation output for epidemic size based on number of infections for recorded movements (top row) and rewired movement networks. The network name denotes the length of the standstill (e.g. 13 days), followed by information on whether the network was rewired to the nearest market (Rw +) or not (Rw -), and lastly whether standstill exemptions were allowed (Ex +), or prohibited (Ex -).

Network	Min.	1 st Qu.	Median	Mean	3rd Qu.	Max.
Recorded	1	55	97	113.6	153	374
13 days Rw- Ex-	1	9	17.5	23.18	30	128
13 days Rw- Ex +	1	40	72	76.41	107	325
13 days Rw + Ex-	1	8	19	26.56	40	120
13 days Rw + Ex +	1	16	49	62.57	88	284
6 days Rw- Ex-	1	16	34	38.53	57	132
6 days Rw- Ex +	1	23	54.5	70.73	103.8	267
6 days Rw + Ex-	1	7	20	29.61	44	152
6 days Rw + Ex +	1	40	62	69.43	94	219

period and also extends to the spatial effects, where we observe a reliable reduction in the number of infections per 10 km^2 grid square for each rewired model run. Importantly, a shorter movement standstill without exemptions is almost as effective as the extreme scenario using a long standstill of 13 days, given that any movement standstill exemptions are prohibited. Nevertheless, a reduction in the length of the standstill period from thirteen days to six days in combination with additional standstill exemptions can result in more rapidly rising disease incidence. Although the simulations presented here do not claim to be completely realistic — a national movement ban would be triggered as soon as a case of FMD is identified on a holding rather than after a fixed period of time—the number of infected holdings can be used as an indicator for the relative impact of legislation changes on the spread of FMD.

Redirecting movements to a different market of the same production type did not seem to affect the epidemic dynamics. However, we did not
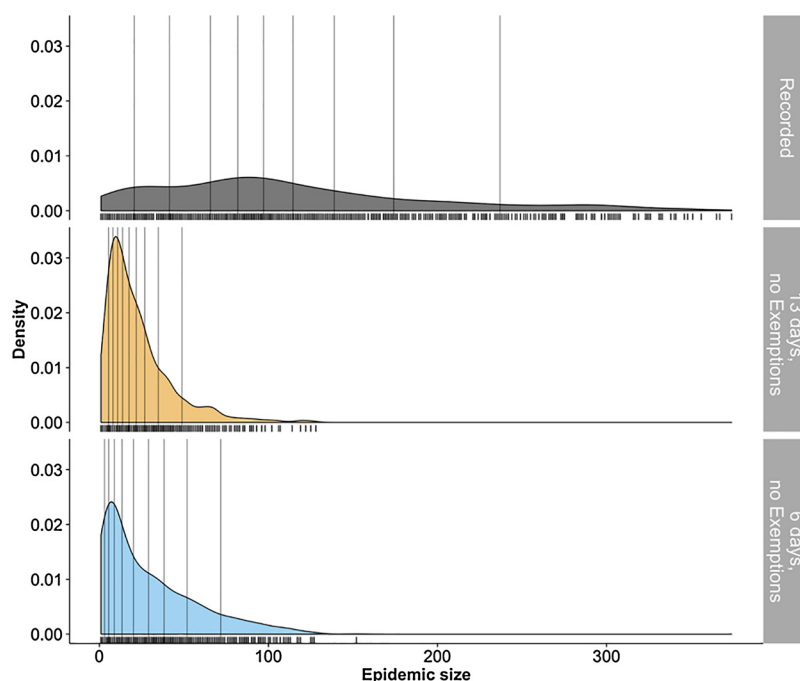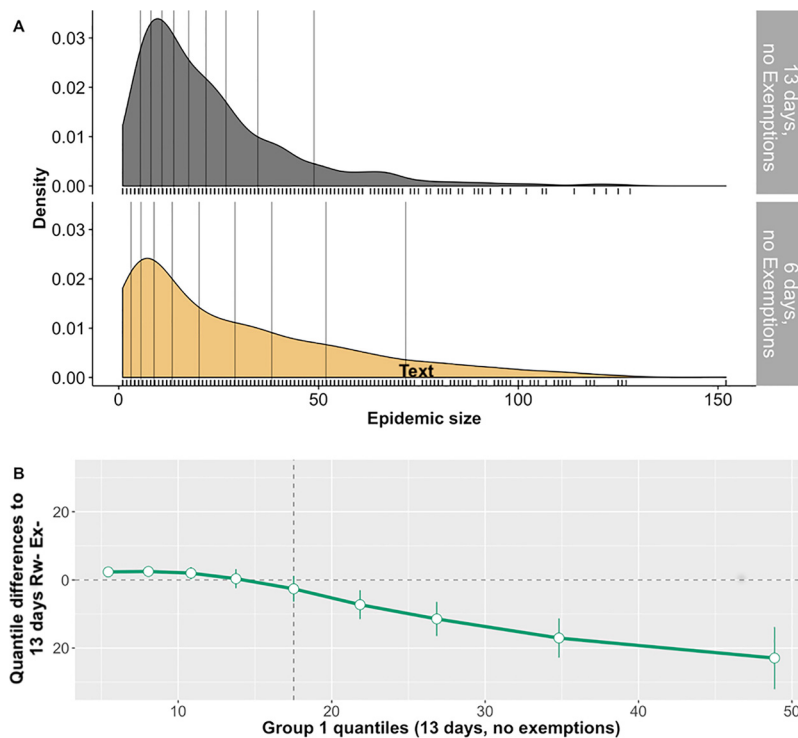

Fig. 4. Kernel density estimates for the output of the FMD simulation on recorded movements (top), the rewired 'extreme' scenario of 13 days standstill with no exemptions (middle), and the rewired 'England-Wales' scenario of 6-day standstill with no exemptions (bottom), with vertical lines representing deciles.

movement restrictions and rewired connections between holdings and markets might affect the final size of a simulated FMD outbreak. From an epidemiological perspective, there is obvious benefit from rewiring, resulting in networks with higher clustering coefficients. As noted above, disease transmission through networks with higher clustering coefficients will show a more rapid reduction of susceptibles (Keeling and Eames, 2005). Hence, if a holding transmits a disease to its two connected neighbours, the number of susceptibles not only decreases for the holding in question, but also for its neighbours. The higher clustering coefficient also leads to lower density for the artificially generated networks compared to the recorded movement network, which in turn also decreases the number of susceptible contacts. Overall, the static network measures appear to be good predictors for the outcome of the simulations, resulting in smaller epidemics on all rewired scenarios.

Investigating the epidemic size for the FMD simulation on the rewired networks compared to the FMD simulation output of the empirically observed network clearly shows that the presence of standstill exemptions will increase the probability of resulting in a larger epidemic size. This effect is independent of the length of the standstill

explicitly consider redirecting links based on the node degree of the markets. Potentially, a finer grained algorithm which aims at minimising the formation of high-risk edges between source premises with a high in-degree and destination premises with a high out-degree as well as the integration of behavioral patterns is necessary. Specifically, redirecting market movements from high-volume markets to markets with less ingoing connections may result in a different simulation outcome. Likewise, holdings with different production types will likely have different contact patterns and the rewiring model could be expanded to include holding specific data.

While the number of premises that appear to be violating legally binding standstill requirements could be high, numerous deficiencies and inconsistencies in the available data prevent the full scope of movements during the standstill period from being appropriately categorised. The greater detail of the CTS database resulted in a greater ability to identify standstill exemptions in cattle. Given that many standstill exemptions refer to individual animal characteristics, we were not able to accurately identify these exemptions for the batched sheep data. However, even in cattle - where we were able to identify almost twice as many apparent standstill exemptions than in sheep - there are

Fig. 5. A. Kernel density estimates for the output of the FMD simulation on the rewired 'extreme' scenario of 13 days standstill with no exemptions (top), and the rewired 'England-Wales' scenario of a 6-day standstill with no exemptions (bottom), with vertical lines representing deciles. **B.** Shift function. The difference of Group 1 (13 days, no exemptions) – group 2 (6 days, no exemptions) is plotted along the y-axis for each decile (white disks), as a function of group 1 deciles. For each decile difference, the vertical line indicates its 95% bootstrap confidence interval (1000 samples). When a confidence interval does not include zero, the difference is considered significant.
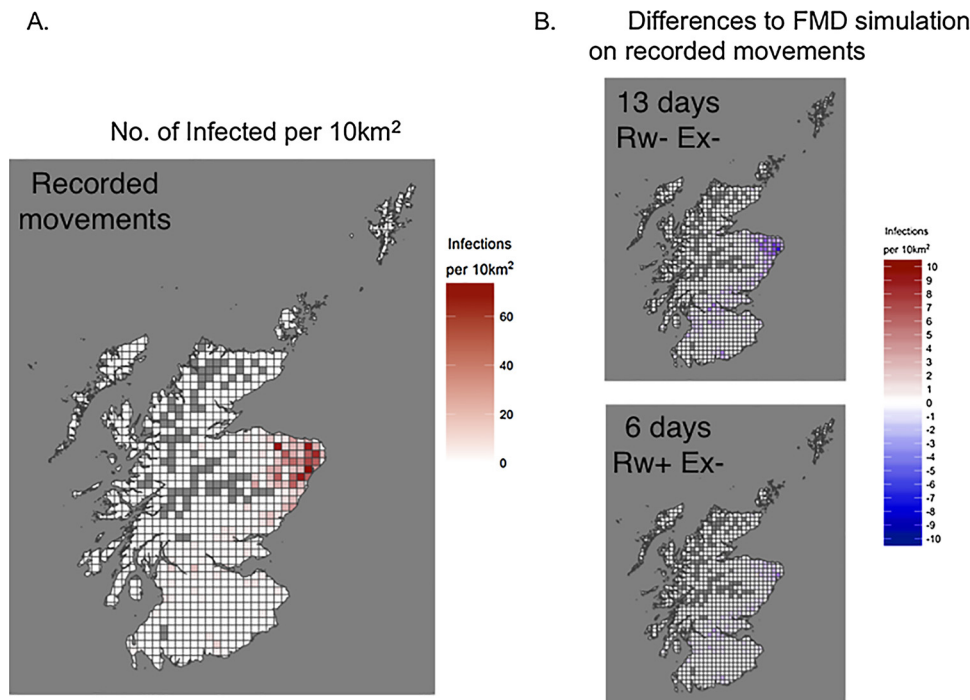
Fig. 6. A. Number of infections per 10 km² for the FMD simulation on the originally recorded cattle and sheep movements. **B.** Differences between the FMD simulations on recorded movements and the rewired 'ideal' scenario (13_days Rw- Ex-, top right) and the rewired 'England / Wales – scenario' (6 days Rw+ Ex-, bottom right). Warmer colours denote an increase in counts, cooler colours denote a decrease of counts.).

still more movements taking place within the first six days of the standstill period that possibly violate mandatory movement restrictions than those which are obviously exempt. This is potentially due to the fact that market days occur every seven days. It is also likely that these movements include many movements that are in fact exempt from the standstill rule, for example due to linked cattle holdings (Enright and Kao, 2016). Some movements violating the standstill restrictions may also result from confusion over the rules (Hunting, 2006), and it may be beneficial to take investigations into farmer behaviour and their perception of the standstill regime into consideration.

5. Conclusions

Our results suggest that explicitly manipulating the contact network structure in a sensible way has the potential to significantly impact disease control. However, any legislation impacting livestock movement patterns could also have undesirable effects such as forcing small markets out of business or even increasing the likelihood of a larger outbreak. Whatever the underlying reasons for violating movement standstills, the large number of movements in an apparent restriction period indicate that a simpler biosecurity system with shorter standstills but no exemptions, which would likely be easier to legislate for and

monitor, would offer no substantial additional risk for FMD.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.prevetmed.2018.05.006.

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