

1 **Models to capture the potential for disease transmission in domestic sheep flocks**

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6 **Abstract**

7 Successful control of livestock diseases requires an understanding of how they spread amongst
8 animals and between premises. Mathematical models can offer important insight into the dynamics
9 of disease, especially when built upon experimental and/or field data. Here the dynamics of a range
10 of epidemiological models are explored in order to determine which models perform best in
11 capturing real-world heterogeneities at sufficient resolution. Individual based network models are
12 considered together with one- and two-class compartmental models, for which the final epidemic
13 size is calculated as a function of the probability of disease transmission occurring during a given
14 physical contact between two individuals. For numerical results the special cases of a viral disease
15 with a fast recovery rate (foot-and-mouth disease) and a bacterial disease with a slow recovery rate
16 (brucellosis) amongst sheep are considered. Quantitative results from observational studies of
17 physical contact amongst domestic sheep are applied and results from the differently structured
18 flocks (ewes with newborn lambs, ewes with nearly weaned lambs and ewes only) compared. These
19 indicate that the breeding cycle leads to significant changes in the expected basic reproduction ratio
20 of diseases. The observed heterogeneity of contacts amongst animals is best captured by full
21 network simulations, although simple compartmental models describe the key features of an
22 outbreak but, as expected, often overestimate the speed of an outbreak. Here the weights of
23 contacts are heterogeneous, with many low weight links. However, due to the well-connected
24 nature of the networks, this has little effect and differences between models remain small. These
25 results indicate that simple compartmental models can be a useful tool for modelling real-world
26 flocks; their applicability will be greater still for more homogeneously mixed livestock, which could
27 be promoted by higher intensity farming practices.

28 **Keywords:** sheep flocks; disease transmission; weighted contact-network; compartmental models;
29 stochastic simulation.

30 1 Introduction

31 Livestock diseases present a challenge to global food security and are of socioeconomic importance
32 both in industrialized nations (e.g. Paarlberg et al., 2008) and the developing world (Perry and Grace,
33 2009; Rushton, 2009). It is important to understand the spread of pathogens amongst animal hosts
34 both for livestock health and productivity and potentially for human health directly, since the
35 majority of emerging infectious diseases are of zoonotic origin (Taylor et al., 2001; Jones et al.,
36 2008).

37 Mathematical models are an established tool in epidemiology, offering qualitative and often
38 quantitative insights into the possible dynamics of diseases. Their potential for helping to
39 understand livestock diseases is particularly strong because of the relatively structured lives of
40 domestic animals (in comparison to, for example, studying wildlife or human interactions).

41 Epidemiological models have already been applied to a number of important diseases, such as foot-
42 and-mouth disease (e.g. Ferguson et al., 2001; Keeling et al., 2001; Keeling, 2005; Tildesley et al.,
43 2006; summary in Schley, 2007; Jewell et al., 2009), Bluetongue (Gubbins et al., 2008; Hendrickx et
44 al., 2008), brucellosis (England et al., 2004) and classical swine fever (Backer et al., 2008). Most,
45 however, only consider disease transmission explicitly on a large scale i.e. between premises, making
46 use of livestock movement data and holding records, while actual transmission data is generally
47 restricted to small scale experiments between a few animals. Although infection between
48 individuals is therefore reasonably well understood for a number of pathogens, it is fallacious to
49 assume that groups of animals will respond in the same way; key temporal factors such as the latent,
50 incubation and infectious periods are likely to be different for herds and flocks than for individual
51 animals.

52 Group level dynamics will be driven by the pattern of interactions between susceptible and
53 infectious hosts, as well as intrinsic properties of the pathogens. How these relate to individual
54 dynamics can be non trivial, especially if behaviour is not homogeneous. The number and relative

55 strength of connections between individuals impacts on the basic reproduction number for an
56 outbreak (Keeling and Grenfell, 2000). These properties, as well as factors such as group size and
57 heterogeneity, determine what theoretical structures (mathematical models) are appropriate in
58 different settings. For example, human contact patterns have been found to be more
59 heterogeneous than assumed by classic homogeneous-mixing models, but “not as variable as some
60 have speculated” (Bansal et al., 2007).

61 While well parameterized network models can provide an accurate description of populations with
62 complex contact structure, they are analytically intractable and less transparent compared to
63 compartmental models. In many situations output from network models is compared to output from
64 low dimensional ODE models, to see if compartmental models could provide an acceptable
65 substitute for full-network simulations. This could significantly reduce computation time for regional
66 simulations in which group models are only one component, and also potentially increase the
67 transparency of complex simulations.

68 It is of practical value to determine what level of model complexity is required to adequately
69 describe realistic scenarios, and where approximating assumptions do not undermine the validity of
70 results. Here field data on physical contact between domestic sheep is applied to a series of models
71 to identify the most suitable mathematical structure for representing disease transmission in flocks.
72 Domestic sheep were selected since they are probably the least intensively farmed animals in the UK
73 and most of Europe, and consequently have the potential to be the least homogeneously mixed,
74 with much less enforced direct or indirect contact than, for example, indoor reared pigs or dairy
75 cattle.

76 **2 Methods**

77 There exist a number of detailed studies on the nature and composition of flocks – for a review see
78 for example Fisher and Matthews (2001) and Nowak et al. (2008) – and previous observations have
79 found age-dependent behaviour amongst sheep, as well as that driven by parenthood. It is

80 therefore appropriate to consider distinct age classes, which in turn necessitates consideration of
81 flocks at different times in the breeding cycle. The models developed here are based upon the
82 amount of physical contact between all individuals within a flock. In addition to generic analytic and
83 numerical results, explicit examples are then derived using data from observational field studies of
84 conventionally managed UK domestic flocks; three different data sets were modelled (from flocks
85 with: young (newborn) lambs and their mothers; older (nearly weaned) lambs and their mothers;
86 mature ewes only) – for details see Supplementary Information section S1 and Table 2.

87 **2.1 Contact rates**

88 Data for each flock is in the form of an adjacency matrix $C = \{c_{ij}\}_{1 \leq i, j \leq N}$: this records the frequency
89 of physical contacts between individuals, where N is the total number of sheep. The resulting
90 matrix is symmetric since a contact between sheep i and sheep j contributes to both c_{ij} and c_{ji}
91 i.e. contacts are not considered directional, with no distinction made between which animal initiated
92 or received the contact. This is an appropriate assumption when considering disease transmission,
93 since it is the contact alone that is important. Where there is no contact between two sheep, the
94 entry is zero (including c_{ii} for $i = 1, \dots, N$). This is not uncommon between ewes, which are known to
95 separate from the flock to give birth (Fisher and Matthews, 2001). For dyads involving lambs we
96 might expect an eventual link if animals are observed for long enough, although in some cases this
97 timescale may be longer than the flock classification, involving growing lambs, is valid for; however,
98 over this time many additional contacts are likely to be made across existing links so that nature of
99 the weighted network would not be significantly altered.

100 This matrix of weighted contacts can be interpreted as a weighted network, where the strength of a
101 link c_{ij} is simply equal to the frequency of contacts between individual i and j . For the purpose of
102 the analysis, all rates have been scaled to units corresponding to the expected number of contacts
103 per day. Figure 1 shows the degree distribution of the within-flock networks by considering every

104 non-zero entry in the contact matrix as a link in the network. Also shown are the per-link weight
105 distributions for each of the three different flocks considered. The networks, in all three situations,
106 are relatively well connected with individuals having a high number of links and with a per-link
107 weight distribution that is skewed towards smaller weights. The implications of these network
108 properties are discussed below.

109 The contact matrix $C = \{c_{ij}\}_{1 \leq i, j \leq N}$ will be the building block for all the within-flock models and will
110 contribute to defining both (i) individual based models that are accurate and account for all the
111 detailed information in the contact matrix and (ii) compartmental models constructed at a group
112 (i.e. ewes and lambs) or whole population (i.e. the entire flock) level. The latter require only
113 group/population metrics that can be obtained by appropriate averaging of all the rates in the full
114 contact matrix. How the data feeds into the stochastic simulation and approximate ODE models is
115 illustrated clearly below.

116 **2.2 Disease dynamics**

117 As there is significant variability in the dynamics of different sheep diseases, results derived here are
118 kept as general as possible. Where appropriate foot-and-mouth disease (FMD), a viral disease with a
119 fast recovery rate of 7-8 days in sheep (Alexandersen et al., 2002), and Brucellosis, a bacterial
120 disease with a slow recovery rate of approximately 3 weeks in sheep (The Center for Food Security
121 and Public Health, 2009) are considered as exemplars: in all cases the parameter ranges presented
122 encompass the respective expected values for both diseases.

123 To provide estimates of the transmission probability between animals for the exemplar FMD, the
124 experimental data of Orsel et al.(2007) is considered. This provides the infection status, at the end
125 of a 14-day trial period, of six groups of four unvaccinated lambs, two of which were initially infected
126 (by inoculation), the other two being susceptible individuals (for details see Orsel et al., 2007).
127 These results are fitted to a stochastic model, together with an estimated recovery time of 7-8 days
128 (Alexandersen et al., 2002) to derive the force of infection, from which the probability of

129 transmission is estimated using the contact data described above – see Supplementary Information
130 section S3 for full details.

131 In all the models that follow, both stochastic simulations on networks, stochastic and deterministic
132 ODEs, the simple SIR paradigm is considered. In this case, an individual moves from being susceptible
133 (S) to being infected and infectious (I) at a rate proportional to the number of infectious contacts
134 it has (in compartmental models this may be formulated in a number of ways; see for example
135 (Begon et al., 2002)). Infectious individuals move to a recovered state (R), where they are immune
136 to further infection (possible because they are dead), at a rate that is independent of the network or
137 state of the population. The SIR dynamic is suitable diseases such as FMD and Brucellosis, and have
138 been previously used in this context – see for example (Keeling et al., 2001; Moutou and Durand,
139 2002) and (England et al., 2004) respectively.

140 **2.3 Individual-based network models**

141 The most comprehensive model makes full use of the contact network data. A network
142 representation of the contact matrix is used, in which each individual (i.e. sheep) is a node in a
143 network. Susceptible individuals are at risk of becoming infected when in contact with at least one
144 infectious individual, with a higher frequency of contact (here given by a higher weighted link
145 between nodes) resulting in a higher transmission rate. For example, in a small time interval δt the
146 probability of a susceptible individual i becoming infected is:

$$147 \quad 1 - \exp\left(-\sum_{j \in \Lambda} p c_{ij} \delta t\right)$$

148 Where $\Lambda = \{k : \text{sheep in class I}; 1 \leq k \leq N\}$ and p is the probability that an individual contact
149 between a susceptible individual and an infectious individual results in transmission. It follows that
150 higher contact rates lead to a higher probability of transmission. Similarly, in the same small time
151 interval, infectious individuals have a probability of recovery equal to:

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$$1 - \exp(-\gamma\delta t).$$

153

Stochastic simulations of the network are updated asynchronously, following the Gillespie algorithm,

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whereby the time to next event, T , is an exponentially distributed random variable chosen from an

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exponential distribution with rate R_T , where R_T is the rate of all possible transitions given the

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current infectious status of all sheep. It follows that working out R_T amounts to summing all the

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infection and recovery rates across the whole network. The inter-event time is directly related to the

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total rate, with large rates resulting in small inter-event times. Once the time to next event is

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determined, a single event out of all possible is chosen at random but proportionally to its rate.

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The large heterogeneity or variance in frequency of contacts across links as well as in the number of

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links that individuals have (see Figure 1) is investigated by setting up network simulation models

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where the contact rate across the network is conserved but weights are distributed equally either

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per group (lambs and ewes) or per flock, either over existing links or over a fully connected flock.

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The closest approximation to true-life behaviour is assumed to be given by the most complex model,

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namely:

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- I. The fully weighted heterogeneous network, as defined by the matrix $C = \{c_{ij}\}_{1 \leq i, j \leq N}$.

167

In addition to the above, the following scenarios are also considered:

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- II. A network with all link conserved but with all contact rates across links being constant and

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equal to the average of all contact rates over the number of existing links:

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$$c_G = \frac{1}{|L|} \sum_{i=1}^N \sum_{j=1}^N c_{ij} \quad \text{where } L = \{c_{ij} : c_{ij} \neq 0\}.$$

171

- III. A semi-homogeneous two-class fully connected network, with all contact rates replaced by

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the group-level means for the daily contact rate between: two ewes (c_e); between two

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lambs (c_l); and between a ewe and a lamb (c_m):

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$$c_e = \frac{1}{N_e(N_e - 1)} \sum_{j \in G_e} \sum_{i \in G_e} c_{ij}, \quad c_l = \frac{1}{N_l(N_l - 1)} \sum_{j \in G_l} \sum_{i \in G_l} c_{ij}, \quad c_m = \frac{1}{N_e N_l} \sum_{j \in G_e} \sum_{i \in G_l} c_{ij},$$

175 Where N_e is the number of ewes, N_l the number of lambs in each flock (with $N_l = 0$ in the
 176 mature flock), giving $N = N_e + N_l$ sheep in total, and G_e and G_l are the set of indices for
 177 ewes and lambs in each matrix respectively (so that $|G_i| = N_i$ for $i = e, l$).

178 IV. A completely homogeneous one-class fully connected network, with all contact rates equal
 179 to the flock mean c :

180
$$c = \frac{1}{N(N - 1)} \sum_{j=1}^N \sum_{i=1}^N c_{ij}.$$

181 In practice $c_G / c = N(N - 1) / |L|$.

182 Comparison of these network models allows us to determine the impact of heterogeneity in contact
 183 and contact weight distribution, as given by the data, on the spread of an epidemic. Of significance
 184 here are the degree and per-link weight distributions for each of the three different flocks being
 185 studied, as shown in Figure 1. The semi- and completely-homogeneous networks also provide
 186 benchmark results for assessing the validity of compartmental models.

187

188 **2.4 Compartmental ODE models**

189 The flock networks described above lend themselves to being modelled using a two-class SIR
 190 ordinary differential equation (ODE) system. Building on work by Kiss et al. (2009), where a two-
 191 group preferential mixing model was formulated from a contact network point of view, a two-class
 192 SIR model representing ewes and lambs is constructed. The force of infection the product of: the
 193 rate of contact k an individual has with the rest of the group; the probability that any given contact
 194 is between a susceptible individual and an infectious individual – here assumed to be frequency

195 dependent i.e. equal to I/N ; and the probability p that such a contact successfully results in
 196 transmission (Begon et al., 2002). The model takes the form:

$$\begin{aligned} \frac{dS_e}{dt} &= -p \left(k_{ee} \frac{I_e}{N_e} + k_{el} \frac{I_l}{N_l} \right) S_e \\ \frac{dS_l}{dt} &= -p \left(k_{le} \frac{I_e}{N_e} + k_{ll} \frac{I_l}{N_l} \right) S_l \\ \frac{dI_e}{dt} &= p \left(k_{ee} \frac{I_e}{N_e} + k_{el} \frac{I_l}{N_l} \right) S_e - \gamma I_e \\ \frac{dI_l}{dt} &= p \left(k_{le} \frac{I_e}{N_e} + k_{ll} \frac{I_l}{N_l} \right) S_l - \gamma I_l \\ \frac{dR_e}{dt} &= \gamma I_e \\ \frac{dR_l}{dt} &= \gamma I_l \end{aligned}$$

198 where the subscripts e and l refer to the ewe and lamb populations and k_{ee} , k_{el} , k_{le} and k_{ll} are
 199 the average contact rates between a ewe and other ewes, a ewe and lambs, a lamb and ewes and a
 200 lamb and other lambs respectively. In the absence of one or other population (e.g. $N_l = 0$) the
 201 system collapses down to the standard single-class model:

$$\begin{aligned} \frac{dS}{dt} &= -pk \frac{I}{N} S \\ \frac{dI}{dt} &= pk \frac{I}{N} S - \gamma I \\ \frac{dR}{dt} &= \gamma I \end{aligned}$$

203 with transmission rate $(pk/N)IS$ (where e.g. the total population $N = N_e$ and there is only a
 204 single contact rate $k = k_{ee}$). This simpler ODE model may also be applied to mixed flocks (consisting
 205 of ewes and lambs, with $N = N_e + N_l$ and contact given by the flock-level average k), but at the
 206 cost of neglecting much of the structure that is present in the individual to group mixing.

207 This group-model is a simplification of the full network description, much more amenable to
 208 analysis, rapid computation and real-life parameterization: below its potential to approximate the
 209 output from the full individual-based simulation is assessed.

210 Note that the mean contact rates $k_{\bullet\bullet}$ are different (but related to) the mean contact rates c_{\bullet} : for
 211 compartmental models it is the total contact an individual has with all members of each group that
 212 determines transmission, rather than the pair-wise contact rates. These group-level rates are
 213 derived from the full weighted contact matrix C by:

$$214 \quad k_{ee} = \frac{1}{N_e} \sum_{i \in G_e} \sum_{j \in G_e} c_{ij}, \quad k_{el} = \frac{1}{N_e} \sum_{i \in G_e} \sum_{j \in G_l} c_{ij}, \quad k_{le} = \frac{1}{N_l} \sum_{i \in G_l} \sum_{j \in G_e} c_{ij}, \quad k_{ll} = \frac{1}{N_l} \sum_{i \in G_l} \sum_{j \in G_l} c_{ij},$$

215 where G_e and G_l are defined as above. For the whole flock average we have

$$216 \quad k = \frac{1}{N} \sum_{i=1}^N \sum_{j=1}^N c_{ij} = (N-1)c.$$

217 Within each flock most contact rates are also significantly different to each other (see
 218 Supplementary Information Table 3 for full details), suggesting that the assumption of homogeneous
 219 contact required by a single class model is not appropriate for breeding flocks. These rates $k_{\bullet\bullet}$ are
 220 also all significantly different between the three different flock types (see Supplementary
 221 Information Table 4 for details), apart from the rate of contact a ewe has with other ewes while she
 222 has lambs, which does not change significantly with the age of the lambs.

223 The following models are considered numerically, for each of the three flocks:

224 V. two-class ODE compartmental model, differentiating ewes and lambs, with group level
 225 contact rates k_{ee} , k_{el} , k_{le} and k_{ll} :

- 226 i. deterministic solution;
- 227 ii. stochastic realization;

228 VI. one-class ODE compartmental model, combining all sheep, with group level contact rate k :

229 i. deterministic solution;

230 ii. stochastic realization;

231 with analytical results presented for V.i and VI.i. Obviously for the ewe-only flock models V and VI
232 are identical.

233 **2.5 Numerical simulations**

234 Although it is assumed that parameters derived from the contact data are applicable to all flock sizes
235 of more than three or four animals (see discussion for limitations), the underlying assumptions of
236 the deterministic model are only truly valid in the limit of large N . Since here disease dynamics are
237 firstly considered amongst a conventional sized flock of only about 30 animals, it is appropriate to
238 quantify the effects of stochasticity on results. Stochastic network and stochastic ODE simulations
239 were implemented through Matlab (MathWorks, 2010), with all results based on 5000 replicates
240 unless stated otherwise. Numerical solutions of the deterministic system were derived using the
241 Matlab routine ode45, but are only considered in relation to analytical results.

242 Disease is seeded in one individual i.e. $I(0)=1$ and $S(0)=N-1$; in the case of networks the
243 individual is chosen at random from the N nodes in the network for each replicate, while for the
244 ODE models a class is chosen at random weighted by the size of each class (i.e. N_e / N and N_l / N).
245 In practice the contact between the ewe and lamb groups is sufficiently strong that there is no
246 significant difference in results on whether it is a ewe or lamb that is initially infected.; an epidemic
247 may result even if k_{ll} , k_{ee} or both are zero, provided that $k_{el} > 0$ (and hence $k_{le} > 0$), since this is
248 sufficient to connect all members of the flock.

249 **2.6 Mathematical analysis**

250 Following the methodology of Van den Driessche and Watmough (2002), which notes that only the
 251 rate at which the number of infectious individuals changes influences R_0 , it can be shown that the
 252 rates at which new infections appear and are removed when the system is in the disease free
 253 equilibrium $(N_e, N_l, 0, 0)$ are given by

$$254 \quad F = P \begin{bmatrix} k_{ee} & k_{el} \frac{N_e}{N_l} \\ k_{le} \frac{N_l}{N_e} & k_{ll} \end{bmatrix} \text{ and } V = \begin{bmatrix} \gamma & 0 \\ 0 & \gamma \end{bmatrix}$$

255 respectively. R_0 is given by the leading eigenvalue of FV^{-1} :

$$256 \quad R_0 = \frac{P}{\gamma} \frac{k_{ee} + k_{ll} + \sqrt{(k_{ee} - k_{ll})^2 + 4k_{el}k_{le}}}{2}$$

257 For the ewe-only flock the conventional form: $R_0 = \frac{P}{\gamma} k$ is applied.

258 The final epidemic size r^∞ is the proportion of the flock that become infected i.e. does not remain in
 259 the susceptible population. For the mixed-model this is given implicitly by:

$$260 \quad r^\infty = \frac{N_e}{N} (1 - \exp(-\varphi_e^\infty)) + \frac{N_l}{N} (1 - \exp(-\varphi_l^\infty))$$

261 where

$$262 \quad \varphi_e^\infty = \frac{P}{\gamma} (k_e (1 - \exp(-\varphi_e^\infty)) + k_m (1 - \exp(-\varphi_l^\infty)))$$

$$\varphi_l^\infty = \frac{P}{\gamma} (k_m (1 - \exp(-\varphi_e^\infty)) + k_l (1 - \exp(-\varphi_l^\infty)))$$

263 For the ewe only flock the standard implicit formula:

264
$$r^\infty = 1 - \exp\left(-\frac{p}{\gamma} k r^\infty\right)$$

265 holds. Although the final proportion infected individuals does not depend on the total population
 266 size N , it is affected by the fraction of the population that is ascribed to each group if the rates of
 267 within-group or between-group contact are different.

268 **3 Results**

269 **3.1 Analytical results from deterministic models**

270 The estimated values of R_0 , as function of the recovery rate γ and the probability of a contact
 271 (between and infected individual and a susceptible one) resulting in transmission p for each of the
 272 trials are given in explicitly in Table 1, but of greatest interest is the relative magnitude of the basic
 273 reproduction number within the flock at different times of the year. This is independent of p
 274 and γ , and shows that the presence of lambs significantly increases physical contacts and that this is
 275 worst when lambs are young:

276
$$\frac{R_0^{\text{with newborns}}}{R_0^{\text{ewes only}}} = 16.1, \quad \frac{R_0^{\text{with weaned}}}{R_0^{\text{ewes only}}} = 4.6.$$

277 Using the conventional (single class) form for R_0 these ratios would be less (13.7 and 4.0
 278 respectively). It is important to note that the increased number of contacts in flocks with ewes is not
 279 purely a result of parent-offspring contacts, but increased interconnectivity overall between and
 280 within the age classes (see Table 2 in Supplementary Material for explicit details), so that the
 281 calculation of R_0 is relevant.

282 The final epidemic size as a consequence of physical contact, as a function of the probability of
 283 successful transmission p is shown in Figure 2. Results indicate that an epidemic is much more
 284 likely to take off in a flock with lambs (increasingly so with younger lambs) and that only in an all
 285 adult flock is it likely that some individuals will remain uninfected. Note that unless the recovery

286 rate γ is exceptionally high, only a very low probability of successful transmission per contact is
287 required to sustain the disease.

288 Epidemic length t^0 is the time of recovery of the last case, since the start of the first case, while the
289 time of peak infectiousness t^* is defined as the time when the largest number of animals are
290 infectious: these may be extracted from simulations by considering the duration for which
291 $I = I_e + I_l \geq 0$ (or, more precisely for the continuous model, some strictly positive threshold value)
292 and the time when $\max_{t \geq 0} \{I\}$ are attained respectively. For the single-class model an analytical
293 solution exists (see for example House and Keeling, 2011 and references therein). Figure 3 presents
294 the median of 1000 stochastic replicates (where there is no ambiguity in the definition of t^0),
295 although numerical simulations of the deterministic system are similar (i.e. near-identical for t^*).
296 Differences in the rates of contact within each flock impact on the length of the outbreak, although
297 the interaction between the probability of infection and the rate of recovery is perhaps more
298 significant. For flocks with lambs infection is predicted to die out without a minor outbreak (or full
299 epidemic) only if the probability of successful transmission on contact p is very low, while for the
300 ewe only flock the parameter landscape is dominated by self-limiting outbreaks unless the disease
301 recover rate is very slow.

302 **3.2 Numerical results from stochastic simulations and model comparisons**

303 Results indicate a strong effect of breeding cycle (i.e. differences between flock types) that appears
304 to hold for both highly pathogenic and low virulence diseases – see Figure 4 for results for a realistic
305 range of p . The presence of lambs facilitates a much quicker spread of the disease and such flocks
306 have a much higher chance of experiencing an epidemic. This is to be expected, given the presence
307 of lambs that are more highly connected and who have a much greater frequency of repeat contacts
308 (see Figure 1), which more than compensates for the reduction in connection between ewes that is
309 seen in breeding flocks compared to ewe-only groups. The number and strength of links decreases

310 as lambs grow older, and amongst mature animals a per contact probability of transmission of an
311 order of magnitude bigger is required in order to achieve an outbreak similar to that observed in a
312 flock with newborn lambs (see Figure 4). Explicitly, for our estimated parameter values for FMD (see
313 Supplementary Information section S3) the system results in die-out amongst mature ewes
314 ($S(t) = S(0) \forall t$), a partial outbreak amongst ewes with nearly-weaned lambs(
315 $S(0) \geq S(t) \geq 0 \forall t$) and an epidemic amongst ewes with new-born lambs ($S(t) \rightarrow 0, t \rightarrow \infty$) on
316 the full weighted network. Figure 4 also shows the predicted epidemic from compartmental
317 systems: results from the ODE models lie well within the 95% confidence intervals for all
318 combinations of flock demographics and the full range of p . There is no significant difference
319 between the one- and two-class models for these parameter values, which represent a highly
320 virulent disease, and so only the two-class solution is shown in Figure 4. Results from and stochastic
321 realisations of the ODEs are closer to the (stochastic) networks than deterministic solutions, as one
322 would expect.

323 The two-class model provides a framework to describe a flock of sheep that contains distinct groups,
324 i.e. both ewes and lambs. Figure 5 gives results for models I – VI (both deterministic and stochastic
325 ODE systems, and the four alternative network models) for a flock of ewes with nearly weaned lamb
326 (the median group in terms of connectivity). This case was chosen as it had the greatest difference
327 between results from the full weighted network simulations and the ODE models i.e. results for
328 flocks at other times in the breeding cycle are much more consistent. All the group-wise
329 approximated networks (models II-IV) predict very similar results, and are all much closer to the ODE
330 outputs (models V-VI) than to the output from the full weighted network simulation (model I): in fact
331 there is little difference between the one- and two-class networks and the stochastic realisation of
332 their counterpart compartmental ODEs, but more so with the deterministic solutions as would be
333 expected. This suggests that the heterogeneity in the contact rates acts to somewhat slow the
334 spread of diseases. The lack of difference between the one-class and two-class ODEs (models V-VI) is

335 due to the very high rates of mixing between the groups and probability of transmission combining
336 to give a strong force of infection.

337 Results for smaller and larger flocks (e.g. derived for 6 to 300 animals) remain consistent with these
338 conclusions.

339 **4 Discussion**

340 Results for a two-class frequency-dependent SIR model, representing ewes and lambs in sheep
341 flocks, have been presented (and compared to the one-class model), including important
342 epidemiological parameters such as the basic reproduction ratio and the final outbreak size, in terms
343 of the disease recovery rate, the contact rates between groups and the probability that transmission
344 occurs following contact between a susceptible and an infectious individual. Application of the
345 models to observational field data indicates that the basic reproduction ratio R_0 increases
346 dramatically in the presence of lambs, an effect that decreases with their age as might be expected.
347 Furthermore, this increase is underestimated if a conventional (single class) formulation of R_0 is
348 used. Flock demographics influence not only how quickly a disease spreads, but also the final
349 epidemic size. It has previously be shown that when the basic reproduction number is kept constant,
350 the final epidemic size in the heterogeneously mixed population is always smaller than in an
351 equivalent homogeneously mixed population (Andreasen, 2011). It is clear here, however, that the
352 absence of lambs contributes significantly to reducing the overall size of the outbreak as a result of
353 their contact dynamics (see Figure 2). These results suggest that variability in the structure (and
354 resultant connectivity) of conventionally managed sheep flocks as a result of the breeding cycle can
355 have a significant impact on the potential spread of directly-transmitted ovine diseases.

356 The output from the ODE models was compared to the output from simulations run on weighted
357 networks derived from observed field data. Although individual based simulations on networks are
358 usually regarded as the most accurate type of model, there are a number of considerations that
359 need to be taken into account when assessing their appropriateness. Firstly, networks are very good

360 at describing situations in which contact patterns between individuals are well defined. For this to be
361 the case, what constitutes a contact as well as who contacts whom needs to be well defined. In this
362 case the level of physical contact between individual animals is appropriately defined by the
363 observational data, although what constitutes a successful transmission is less clear. For example,
364 during data collection, each observed contact was weighted equally, regardless of the type of
365 contact (e.g. head but, rub etc) or duration, although the vast majority were short lived contacts.
366 This means that the rates given in the full contact matrix are the approximations for the expected
367 number of individual short lived contacts between two sheep, regardless of type. This differs from,
368 for example, a sexual contact network, in which the contact between individuals is such that there is
369 a more clearly defined possibility of disease transmission. For the short lived contacts recorded here
370 it is less clear if disease transmission, given contact, is possible. Modelling using networks assumes
371 frequency dependent contact which is independent of population size (Begon et al., 2002). Whether
372 a frequency or density dependent approach should be used depends heavily on the flock setup and
373 how it is managed: for example, if the flock is roaming on open hillside then a frequency dependent
374 approach seems suitable. However, if the flock was rounded up and kept in a tight pen, then a
375 density dependent approach would seem more suitable, as each the number of contacts would
376 depend upon how many were in the pen (see Supplementary Information section S4 for further
377 details justifying the formulation adopted here).

378 In general, as graphs become more densely connected, the results from stochastic simulations on
379 graphs tend to approach the mean-field approximation, given by ODE models (Simon et al., 2010),
380 which is exactly the situation shown in Figure 4 and Figure 5. As expected, for a very high
381 (potentially unrealistically) probability of transmission per contact the differences are less significant,
382 since in this case almost all individuals become infected rapidly. It is interesting to note that the full
383 network simulation is markedly more different from the mean-field result than the homogeneous or
384 semi-homogeneous network models. Since the main difference between the various network
385 models lies in the distribution of contacts, the observed differences shown in Figure 5 must be

386 driven by it. The difference between the output from homogeneous and heterogeneous networks
387 can be explained intuitively as follows. Links with high weight are relatively rare (as detailed in Figure
388 1) and hence they will play a minor role in the overall dynamics, which is going to be dominated by
389 links with low weights. This leads to slower dynamics and smaller epidemics. However, when the
390 contribution of highly weighted links is spread evenly across all links, the previously numerous low-
391 weight links become more potent in transmitting the infection and this leads to both faster and
392 larger epidemics.

393 It appears that differences in contact structure and frequency can always be compensated for in this
394 network by adjustments in the per-contact probability of infection p , to produce similarly behaving
395 outbreaks in different flocks. A close inspection of the subplots on the main diagonal of Figure 4
396 shows a very similar time evolution of the epidemic, which suggests that the fundamental structure
397 of the networks is similar, despite the huge variability in the weight of the contacts that are present
398 (both in degree and per-link weights). While the full network simulation best captures the observed
399 heterogeneity of contacts amongst animals, the simpler compartmental models describe the key
400 features of an outbreak. Deterministic solutions over-predict the speed and scale of an outbreak,
401 but fall well within the 95% confidence intervals predicted by the full simulation, with stochastic
402 realisations considerably closer still.

403 Full network simulations of observed flocks indicate that the differences in the predicted disease
404 dynamics between the single-class and two-class models are small when the group as a whole is
405 strongly connected, as appears to be the case for grazing sheep. Furthermore, conventional sized
406 flocks of the size modelled here are sufficiently small for stochastic effects to be important, with
407 stochastic realisations as opposed to deterministic solutions of compartmental models comparing
408 favourably with the network simulations. Although the actual flock sizes simulated here were small,
409 the modelling and the use of data are applicable to flocks of different sizes, at least where contact is
410 optional (as opposed to a result of overcrowding), given the known social behaviour of sheep and

411 the conditions under which data was collected (see summary in Supplementary Information Section
412 S1, or Norton et al. (2011) for full details). Unless space is restricted and resources are limited,
413 group size does not have a large impact on social behaviour (Fisher and Matthews 2001) or grazing
414 (Penning et al., 1993) provided there are not less than four animals. Sheep place social bonds above
415 food preferences (Sibbald et al., 2008), with distance between individuals is not correlated with
416 range size provided there is sufficient grazing (Crofton, 1958).

417 These results indicate that simple compartmental models can be a useful tool for modelling real-
418 world flocks; their applicability will be greater still for more homogeneously mixed livestock, such as
419 might be expected with higher intensity farming practices.

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509

510 **Tables**

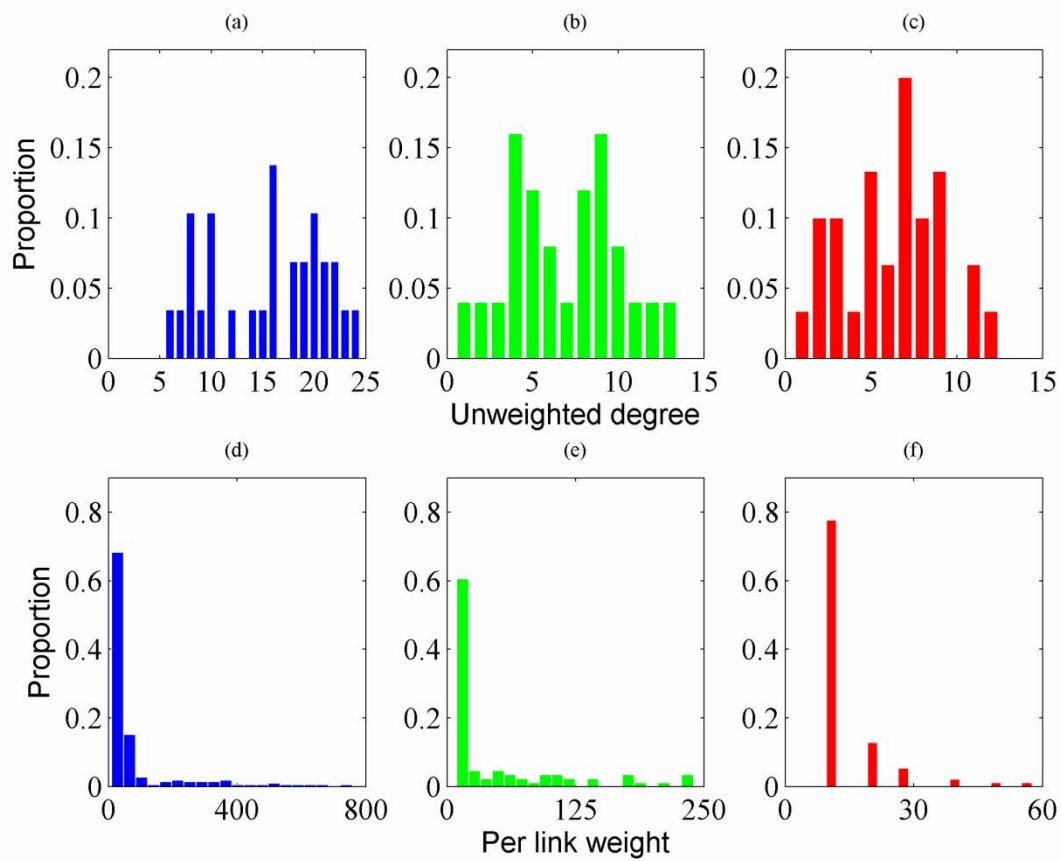
511 *Table 1. Estimated R_0 of whole flock based on the average number of physical contacts per day for*
512 *ewes and lambs; here γ is the recovery rate and p is the probability of a contact (between and*
513 *infected individual and a susceptible one) resulting in transmission.*

| Flock | R_0 |
|-------------------------------|-------------------------|
| Ewes with newborn lambs | 1171 p / γ |
| Ewes with nearly weaned lambs | 344 p / γ |
| Ewes only | 84 p / γ |

514 **Figures**

515

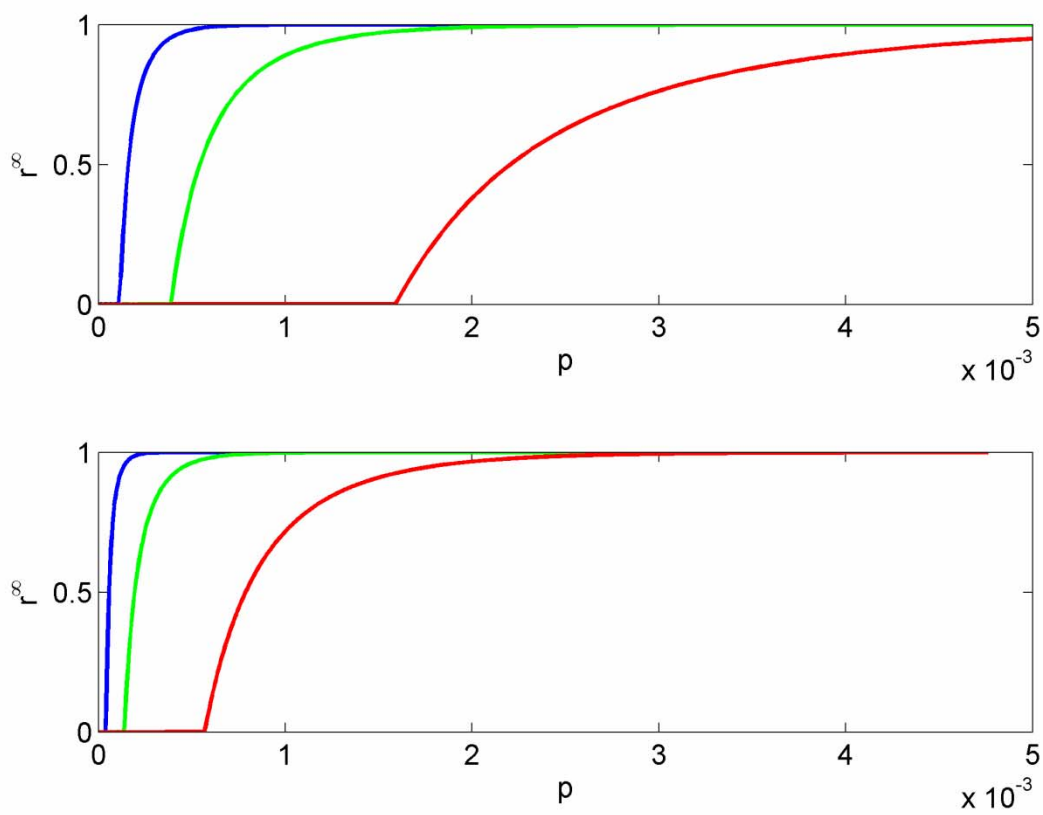
516 *Figure 1. The degree distribution (top row) and per-link weight distribution*
517 *(bottom row) for the three flocks: (a & d) ewes and newborn lambs (blue); (b & e) ewes*
518 *and nearly-weaned lambs (green); and (c & f) ewes only (red). The mean degree for*
519 *each scenario is (a) 14.5; (b) 6.9; and (c) 6.3; the mean per-link weight for each flock is*
520 *(d) 74.3; (e) 49.0 and (f) 13.4.*



521

522

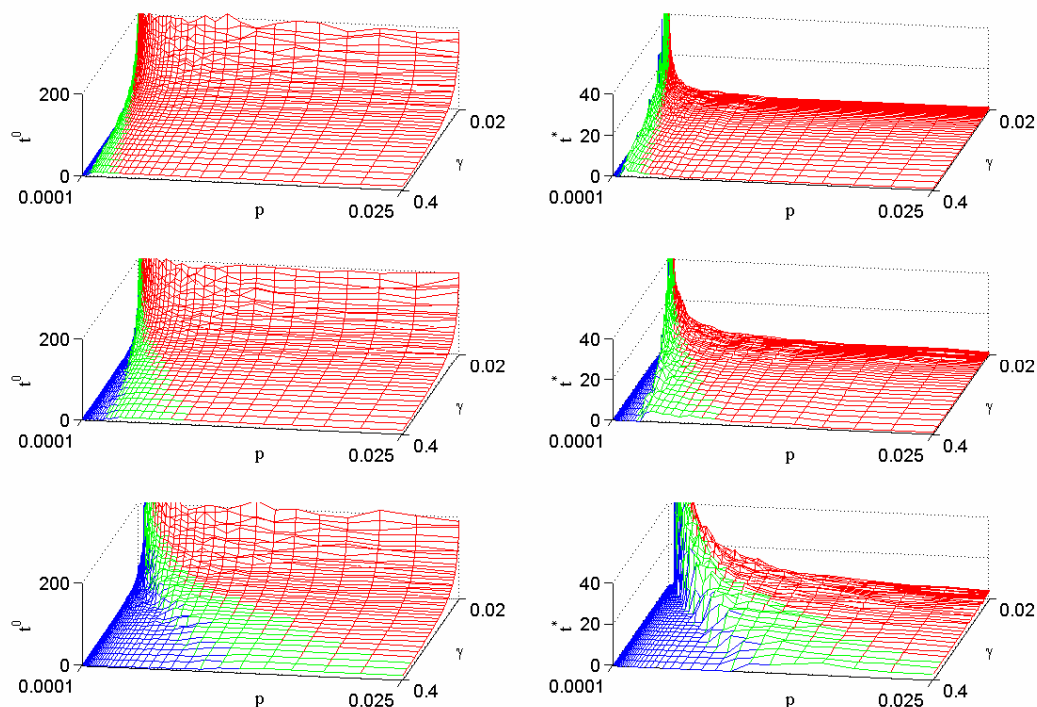
523 *Figure 2. Final epidemic size r^∞ , as a function of the transmission probability p*
524 *for physical contacts amongst a flock with (top) a fast recovery rate similar to FMD*
525 *($\gamma = 2/15$) and (bottom) a slower recovery similar to brucellosis ($\gamma = 1/21$) for: ewes*
526 *with newborn lambs (blue), ewes with nearly weaned lambs (green) and ewe only (red)*
527 *flocks in a conventional group with two lambs per ewe on average.*



528

529

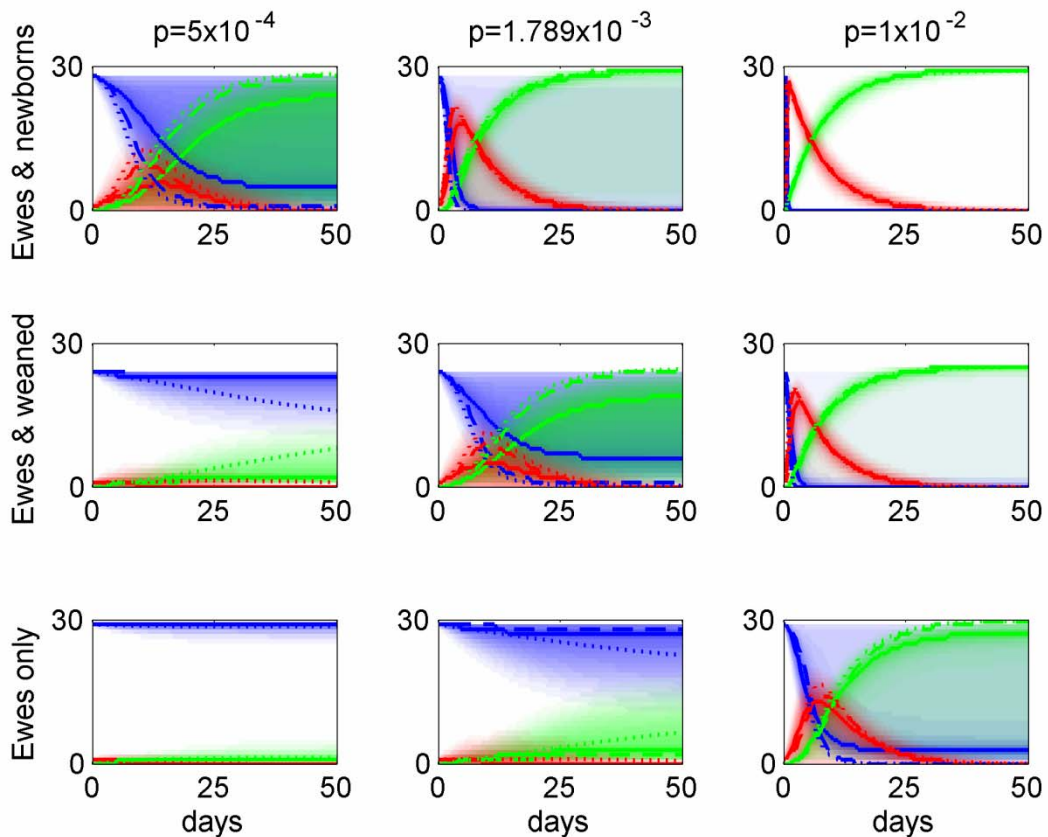
530 *Figure 3. Epidemic length t^0 (left column) and time of peak infectiousness t^* (right*
531 *column) in days, as a function of the recovery rate γ and the transmission probability*
532 *p for physical contacts amongst a flock of 30 sheep consisting of: 10 ewes with 20*
533 *newborn lambs (top), 10 ewes with 20 nearly weaned lambs (middle) and 30 ewes only*
534 *(bottom), based on initial infection of a single ewe. Results are derived from the*
535 *median of 1000 replicates of the stochastic two-class (or one-class where appropriate)*
536 *ODE system, and distinguished according to whether infections die out (blue:*
537 *$S(t)=S(0) \forall t$), result in partial outbreaks (green: $S(0) \geq S(t) \geq 0 \forall t$) or cause*
538 *epidemics that infect the entire flock (red: $S(t) \rightarrow 0, t \rightarrow \infty$). When infection dies out,*
539 *peak infectiousness occurs at the outset of the outbreak ($t^* = 0$) by definition.*



540

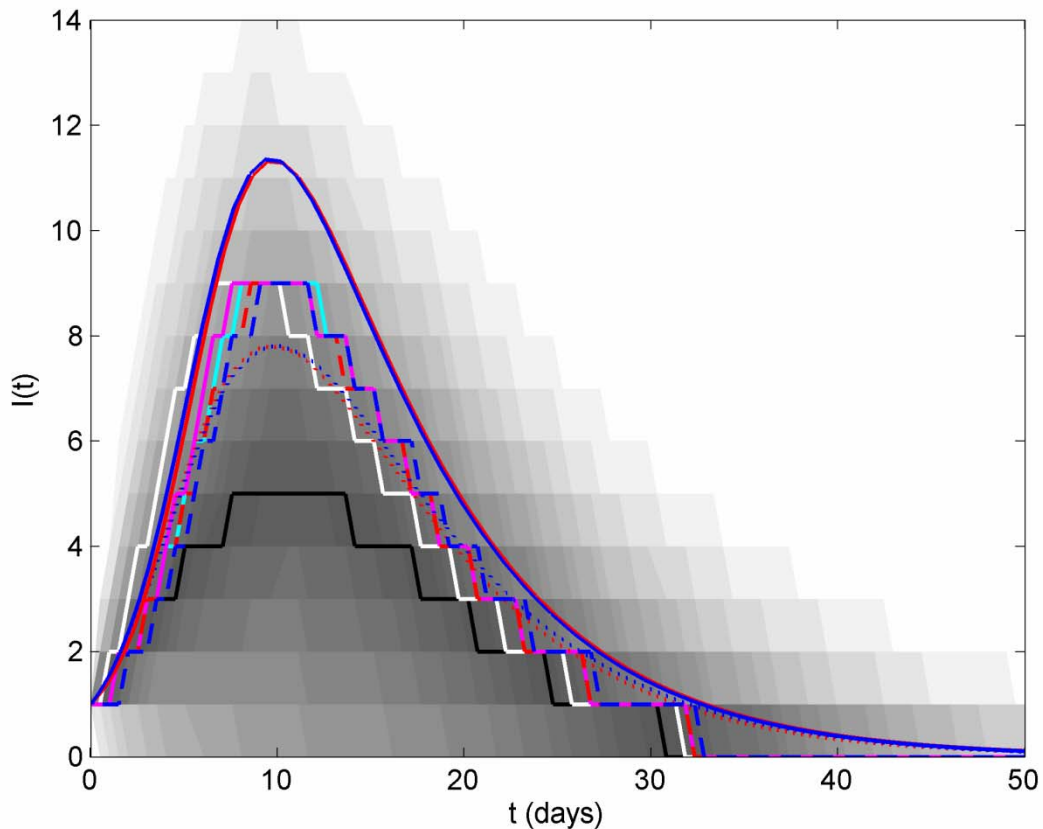
541

542 *Figure 4. The time evolution of a potential outbreak amongst the three different*
543 *flocks (top row: ewes with new-born lambs; middle row: ewes with nearly weaned*
544 *lambs; bottom row: ewes only). Here $\gamma=2/15$, appropriate for FMD, and results are*
545 *presented for three different values of p (the probability of transmission occurring*
546 *during contact): the estimated value for FMD (middle column) and values an order of*
547 *magnitude smaller (left column) and larger (right column) than this. The total number*
548 *of susceptible S (blue), infected I (red) and recovered R (green) individuals is plotted*
549 *as a function of time: the solid lines show the median values from stochastic*
550 *simulations of the full weighted network, with the shaded bands showing confidence*
551 *intervals in steps of 5%. The dashed line shows results from stochastic simulations of the*
552 *two-class ODE (or one-class where appropriate) system, while the dotted line gives*
553 *results from the deterministic equations. Note that the number of ewes and lambs is*
554 *as in the field trials, and varies slightly for each flock (see Supplementary Information*
555 *section S1 for details).*



556

558 *Figure 5. Time evolution of the number of infected for ewes with nearly-weaned*
 559 *lambs (here $N=25$) for $\gamma=2/15$ and $p=1.789\times 10^{-3}$, the estimated recovery rate and*
 560 *probability of transmission per contact respectively for FMD (see text). For all*
 561 *network models, the median number of infected individuals is shown: the black line*
 562 *shows the results from simulations on the full weighted network (model I), with the*
 563 *grey shaded bands showing confidence intervals in steps of 5%; the white line*
 564 *represents simulations on a network that is heterogeneous in the number of contacts,*
 565 *but homogeneous in contacts rates (model II); the magenta line shows results a semi-*
 566 *homogeneous two-class fully connected network, with the contact rates being the*
 567 *appropriate group averages (model III); the cyan line shows results from a*
 568 *homogeneous fully connected network, with the contact rates being the population*
 569 *average (model IV); the blue and red lines represent results from the two-class ODE*
 570 *(model V) and one-class ODE (model VI) respectively, with a solid line for the*
 571 *deterministic solution, a dashed lined for the median of the stochastic results and a*
 572 *dotted line for the mean of the stochastic results.*



574 **Supplementary Information**

575 ***S1. Flock data***

576 Data is taken from the observational field studies of sheep flocks in the UK (Norton et al., 2011).
577 Three distinct flocks were considered: eleven ewes with eighteen young lambs (the latter only a
578 couple of weeks old); the same flock less fallen stock some time later, consisting of ten ewes with
579 fifteen older lambs (just prior to weaning); and a mixed-age flock of thirty mature breeding ewes
580 only. Sheep were a mixture of Dorset and Dorset-cross and grazed in 1.7-2.3 hectare paddocks,
581 which is representative of conventional farming practice. Data was collected using focal animal
582 sampling, which is recommended for relatively unbiased data (Altmann, 1974). This has been found
583 to be accurate for livestock behaviour observations provided a sufficient proportion of all animals is
584 observed (Mitlohner et al., 2001), and was applied to the whole group. Each flock was observed for
585 approximately six hours per day for fifteen days over a three to four week period, with each
586 individual animal in the flock the focus of observations for a randomly allocated ten minute window
587 per day. Thus only a subset of dyads could be observed at any one time (specifically those involving
588 the focus animal) but every animal was part of at least one observed dyad at any time and any
589 animal could record a contact at any time. All physical contacts between individuals (consisted of
590 sniffing, head-butting, suckling or attempted suckling, mounting, pawing, standing astride, rubbing
591 or resting on) were recorded, irrespective of which animal initiated the contact. Results, scaled to
592 the expected number of physical contacts per day for each dyad, are given in Table 2.

593

594 Table 2. Weighted contact matrices for physical contact amongst different flocks, from (Norton et al., 2011); here letter-number combinations (e.g. G1, B3)
 595 refer to individual ewes with suffix letters (a, b) referring to their respective lamb(s).

2A Expected number of physical contacts per days in a flock of ewes with newborn lambs

| | G1 | G1a | G1b | G2 | G2a | G2b | G3 | G3a | G3b | G4 | G4a | G4b | G5 | G5a | G5b | B1 | B1a | B1b | B2 | B2a | B3 | B3a | B4 | B4a | B5 | B5a | B8 | B8a | B8b |
|-----|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| G1 | 0 | 585.6 | 384 | 0 | 0 | 28.8 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19.2 | 19.2 | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 |
| G1a | 585.6 | 0 | 249.6 | 38.4 | 9.6 | 57.6 | 28.8 | 48 | 28.8 | 0 | 19.2 | 0 | 9.6 | 9.6 | 38.4 | 19.2 | 28.8 | 105.6 | 0 | 0 | 48 | 19.2 | 0 | 0 | 0 | 19.2 | 0 | 0 | 9.6 |
| G1b | 384 | 249.6 | 0 | 57.6 | 19.2 | 67.2 | 9.6 | 28.8 | 9.6 | 0 | 48 | 9.6 | 0 | 19.2 | 48 | 19.2 | 9.6 | 57.6 | 0 | 86.4 | 0 | 76.8 | 19.2 | 19.2 | 0 | 0 | 0 | 76.8 | 38.4 |
| G2 | 0 | 38.4 | 57.6 | 0 | 345.6 | 681.6 | 9.6 | 9.6 | 0 | 0 | 9.6 | 0 | 0 | 19.2 | 48 | 0 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 28.8 |
| G2a | 0 | 9.6 | 19.2 | 345.6 | 0 | 307.2 | 0 | 0 | 0 | 374.4 | 28.8 | 38.4 | 0 | 76.8 | 28.8 | 0 | 9.6 | 9.6 | 0 | 0 | 19.2 | 9.6 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 9.6 |
| G2b | 28.8 | 57.6 | 67.2 | 681.6 | 307.2 | 0 | 9.6 | 9.6 | 57.6 | 0 | 28.8 | 28.8 | 0 | 67.2 | 19.2 | 0 | 9.6 | 0 | 0 | 57.6 | 0 | 38.4 | 9.6 | 38.4 | 19.2 | 57.6 | 0 | 9.6 | 19.2 |
| G3 | 0 | 28.8 | 9.6 | 9.6 | 0 | 9.6 | 0 | 758.4 | 441.6 | 0 | 0 | 9.6 | 0 | 28.8 | 0 | 0 | 0 | 9.6 | 0 | 182.4 | 9.6 | 19.2 | 9.6 | 28.8 | 0 | 9.6 | 0 | 0 | 19.2 |
| G3a | 9.6 | 48 | 28.8 | 9.6 | 0 | 9.6 | 758.4 | 0 | 316.8 | 96 | 48 | 38.4 | 67.2 | 48 | 28.8 | 9.6 | 105.6 | 9.6 | 28.8 | 28.8 | 19.2 | 28.8 | 9.6 | 48 | 0 | 0 | 0 | 9.6 | 9.6 |
| G3b | 0 | 28.8 | 9.6 | 0 | 0 | 57.6 | 441.6 | 316.8 | 0 | 38.4 | 0 | 9.6 | 9.6 | 76.8 | 19.2 | 0 | 9.6 | 19.2 | 0 | 0 | 0 | 19.2 | 0 | 9.6 | 0 | 19.2 | 0 | 0 | 9.6 |
| G4 | 0 | 0 | 0 | 0 | 374.4 | 0 | 0 | 96 | 38.4 | 0 | 547.2 | 624 | 0 | 9.6 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 38.4 | 0 | 0 | 0 | 0 | 9.6 |
| G4a | 0 | 19.2 | 48 | 9.6 | 28.8 | 28.8 | 0 | 48 | 0 | 547.2 | 0 | 230.4 | 0 | 9.6 | 9.6 | 0 | 9.6 | 48 | 9.6 | 19.2 | 0 | 38.4 | 9.6 | 76.8 | 0 | 9.6 | 0 | 0 | 28.8 |
| G4b | 0 | 0 | 9.6 | 0 | 38.4 | 28.8 | 9.6 | 38.4 | 9.6 | 624 | 230.4 | 0 | 0 | 28.8 | 9.6 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 0 | 19.2 | 19.2 | 9.6 | 28.8 | 0 | 0 |
| G5 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 67.2 | 9.6 | 0 | 0 | 0 | 0 | 355.2 | 288 | 0 | 9.6 | 28.8 | 0 | 0 | 0 | 28.8 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 0 |
| G5a | 0 | 9.6 | 19.2 | 19.2 | 76.8 | 67.2 | 28.8 | 48 | 76.8 | 9.6 | 9.6 | 28.8 | 355.2 | 0 | 480 | 0 | 28.8 | 57.6 | 0 | 19.2 | 0 | 38.4 | 0 | 28.8 | 57.6 | 9.6 | 0 | 0 | 0 |
| G5b | 0 | 38.4 | 48 | 48 | 28.8 | 19.2 | 0 | 28.8 | 19.2 | 0 | 9.6 | 9.6 | 288 | 480 | 0 | 0 | 28.8 | 105.6 | 0 | 19.2 | 0 | 0 | 0 | 28.8 | 0 | 0 | 0 | 0 | 86.4 |
| B1 | 0 | 19.2 | 19.2 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 268.8 | 288 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 0 | 0 | 38.4 |
| B1a | 19.2 | 28.8 | 9.6 | 0 | 9.6 | 9.6 | 0 | 105.6 | 9.6 | 9.6 | 9.6 | 0 | 9.6 | 28.8 | 28.8 | 268.8 | 0 | 518.4 | 0 | 38.4 | 0 | 144 | 0 | 0 | 0 | 48 | 0 | 0 | 67.2 |
| B1b | 19.2 | 105.6 | 57.6 | 0 | 9.6 | 0 | 9.6 | 9.6 | 19.2 | 0 | 48 | 0 | 28.8 | 57.6 | 105.6 | 288 | 518.4 | 0 | 19.2 | 28.8 | 19.2 | 48 | 9.6 | 48 | 0 | 0 | 57.6 | 57.6 | 28.8 |
| B2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 28.8 | 0 | 0 | 9.6 | 19.2 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 384 | 0 | 0 | 9.6 | 19.2 | 0 | 0 | 0 | 0 | 9.6 |
| B2a | 9.6 | 0 | 86.4 | 19.2 | 0 | 57.6 | 182.4 | 28.8 | 0 | 0 | 19.2 | 0 | 0 | 19.2 | 19.2 | 0 | 38.4 | 28.8 | 384 | 0 | 9.6 | 19.2 | 28.8 | 19.2 | 9.6 | 28.8 | 38.4 | 0 | 9.6 |
| B3 | 0 | 48 | 0 | 0 | 19.2 | 0 | 9.6 | 19.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 9.6 | 0 | 230.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| B3a | 0 | 19.2 | 76.8 | 0 | 9.6 | 38.4 | 19.2 | 28.8 | 19.2 | 9.6 | 38.4 | 0 | 28.8 | 38.4 | 0 | 9.6 | 144 | 48 | 0 | 19.2 | 230.4 | 0 | 9.6 | 28.8 | 19.2 | 48 | 28.8 | 9.6 | 76.8 |
| B4 | 0 | 0 | 19.2 | 0 | 9.6 | 9.6 | 9.6 | 9.6 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 28.8 | 0 | 9.6 | 0 | 499.2 | 0 | 9.6 | 0 | 9.6 | 9.6 |
| B4a | 9.6 | 0 | 19.2 | 9.6 | 0 | 38.4 | 28.8 | 48 | 9.6 | 38.4 | 76.8 | 19.2 | 0 | 28.8 | 28.8 | 0 | 0 | 48 | 19.2 | 19.2 | 0 | 28.8 | 499.2 | 0 | 0 | 249.6 | 9.6 | 0 | 57.6 |
| B5 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 57.6 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 19.2 | 0 | 0 | 0 | 211.2 | 0 | 0 | 0 |
| B5a | 0 | 19.2 | 0 | 0 | 0 | 57.6 | 9.6 | 0 | 19.2 | 0 | 9.6 | 9.6 | 9.6 | 9.6 | 0 | 9.6 | 48 | 0 | 0 | 28.8 | 0 | 48 | 9.6 | 249.6 | 211.2 | 0 | 19.2 | 182.4 | 163.2 |
| B8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 28.8 | 9.6 | 0 | 0 | 0 | 0 | 57.6 | 0 | 38.4 | 0 | 28.8 | 0 | 9.6 | 0 | 19.2 | 0 | 412.8 | 336 |
| B8a | 0 | 0 | 76.8 | 0 | 9.6 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 57.6 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 0 | 182.4 | 412.8 | 0 | 211.2 |
| B8b | 0 | 9.6 | 38.4 | 28.8 | 9.6 | 19.2 | 19.2 | 9.6 | 9.6 | 9.6 | 28.8 | 0 | 0 | 0 | 86.4 | 38.4 | 67.2 | 28.8 | 9.6 | 9.6 | 0 | 76.8 | 9.6 | 57.6 | 0 | 163.2 | 336 | 211.2 | 0 |

2B Expected number of physical contacts per days in a flock of ewes with nearly weaned lambs

| | G1 | G1a | G1b | G3 | G3a | G3b | G4 | G4a | G4b | G5 | G5a | G5b | B1 | B1a | B1b | B2 | B2a | B3 | B3a | B4 | B4a | B5 | B5a | B8 | B8b |
|-----|------|-------|-------|-------|-------|-------|-------|-------|------|-------|-------|------|-------|------|-------|-------|-------|-------|-------|------|------|-------|-------|------|------|
| G1 | 0 | 57.6 | 96 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 9.6 | 19.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| G1a | 57.6 | 0 | 172.8 | 0 | 0 | 0 | 0 | 19.2 | 9.6 | 0 | 0 | 0 | 0 | 0 | 105.6 | 0 | 19.2 | 0 | 0 | 0 | 76.8 | 0 | 0 | 0 | 19.2 |
| G1b | 96 | 172.8 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 9.6 | 0 | 9.6 | 19.2 | 0 | 48 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 0 | 0 |
| G3 | 0 | 0 | 0 | 0 | 48 | 105.6 | 19.2 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 28.8 | 19.2 | 0 | 0 | 19.2 | 38.4 | 0 | 0 | 0 | 57.6 |
| G3a | 0 | 0 | 0 | 48 | 0 | 172.8 | 0 | 9.6 | 0 | 0 | 0 | 28.8 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 9.6 | 144 | 19.2 | 0 | 19.2 | 19.2 |
| G3b | 0 | 0 | 0 | 105.6 | 172.8 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 |
| G4 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 172.8 | 240 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| G4a | 9.6 | 19.2 | 19.2 | 9.6 | 9.6 | 0 | 172.8 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 86.4 | 0 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 9.6 |
| G4b | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 240 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 19.2 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 9.6 |
| G5 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 115.2 | 96 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| G5a | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 115.2 | 0 | 67.2 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| G5b | 19.2 | 0 | 9.6 | 0 | 28.8 | 0 | 0 | 0 | 0 | 96 | 67.2 | 0 | 0 | 0 | 48 | 0 | 38.4 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 |
| B1 | 0 | 0 | 19.2 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 240 | 115.2 | 0 | 0 | 0 | 28.8 | 0 | 0 | 0 | 9.6 | 0 | 0 |
| B1a | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 240 | 0 | 9.6 | 0 | 19.2 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 |
| B1b | 0 | 105.6 | 48 | 0 | 0 | 0 | 19.2 | 9.6 | 0 | 0 | 0 | 48 | 115.2 | 9.6 | 0 | 0 | 57.6 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 0 |
| B2 | 0 | 0 | 0 | 28.8 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 230.4 | 0 | 19.2 | 0 | 0 | 0 | 0 | 0 | 0 |
| B2a | 0 | 19.2 | 0 | 19.2 | 0 | 0 | 0 | 86.4 | 19.2 | 0 | 9.6 | 38.4 | 0 | 19.2 | 57.6 | 230.4 | 0 | 0 | 9.6 | 0 | 28.8 | 0 | 0 | 0 | 9.6 |
| B3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 211.2 | 0 | 0 | 0 | 0 | 0 | 0 |
| B3a | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 28.8 | 0 | 0 | 19.2 | 9.6 | 211.2 | 0 | 0 | 0 | 0 | 9.6 | 0 | 9.6 |
| B4 | 0 | 0 | 0 | 19.2 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 192 | 0 | 0 | 0 | 0 |
| B4a | 0 | 76.8 | 0 | 38.4 | 144 | 0 | 0 | 9.6 | 19.2 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 28.8 | 0 | 0 | 192 | 0 | 0 | 0 | 9.6 | 48 |
| B5 | 0 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 105.6 | 0 | 0 |
| B5a | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 105.6 | 0 | 0 | 96 |
| B8 | 0 | 0 | 0 | 0 | 19.2 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 144 |
| B8b | 0 | 19.2 | 0 | 57.6 | 19.2 | 0 | 0 | 9.6 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 9.6 | 0 | 9.6 | 0 | 48 | 0 | 96 | 144 | 0 |

2C Expected number of physical contacts per days in a flock of mature ewes only

| | B1 | B2 | B3 | B4 | B5 | B6 | B7 | B8 | B9 | B10 | G1 | G2 | G3 | G4 | G5 | G6 | G7 | G8 | G9 | G10 | R1 | R2 | R3 | R4 | R5 | R6 | R7 | R8 | R9 | R10 | |
|-----|------|------|-----|-----|------|-----|------|-----|------|------|------|-----|------|-----|------|------|------|-----|------|------|------|------|------|------|-----|------|------|-----|-----|-----|---|
| B1 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 28.8 | 0 | 9.6 | 9.6 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | |
| B2 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 0 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 0 | |
| B3 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | |
| B4 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| B5 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 9.6 | 0 | 0 | 9.6 | 19.2 | 0 | 0 | 19.2 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | |
| B6 | 0 | 9.6 | 9.6 | 9.6 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 9.6 | 0 | 0 | 0 | |
| B7 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 28.8 | 0 | 0 | 0 | 19.2 | 0 | 19.2 | 19.2 | 9.6 | 0 | 0 | 0 | 9.6 | 19.2 | 0 | 0 | 9.6 | 0 | 19.2 | 0 | 9.6 | 0 | |
| B8 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | |
| B9 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 28.8 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 0 | 0 | 0 | 0 | 57.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | |
| B10 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 9.6 | 28.8 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 0 | |
| G1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| G2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| G3 | 0 | 0 | 0 | 0 | 9.6 | 0 | 19.2 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 28.8 | 9.6 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 9.6 | 0 | |
| G4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | |
| G5 | 0 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 9.6 | 0 | 19.2 | 0 | 0 | 0 | 0 | 9.6 | 0 | 9.6 | 28.8 | 0 | 0 | 0 | 0 | 38.4 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | |
| G6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 19.2 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 9.6 | 0 | 0 | 0 | 19.2 | 0 | 19.2 | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | |
| G7 | 0 | 0 | 0 | 0 | 19.2 | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 0 | 9.6 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | |
| G8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| G9 | 28.8 | 19.2 | 0 | 0 | 0 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 0 | 28.8 | 0 | 28.8 | 19.2 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | |
| G10 | 0 | 0 | 0 | 0 | 19.2 | 0 | 0 | 9.6 | 0 | 9.6 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 48 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 9.6 | 0 | |
| R1 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 0 | 57.6 | 28.8 | 0 | 9.6 | 0 | 0 | 0 | 19.2 | 19.2 | 0 | 9.6 | 48 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | |
| R2 | 9.6 | 0 | 0 | 0 | 0 | 0 | 19.2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | |
| R3 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 38.4 | 0 | 0 | 9.6 | 0 | |
| R4 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 38.4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| R5 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | |
| R6 | 0 | 9.6 | 9.6 | 0 | 9.6 | 9.6 | 0 | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 0 | 38.4 | 0 | 0 | 0 | 9.6 | 9.6 | 9.6 | 0 | 0 |
| R7 | 0 | 0 | 0 | 0 | 0 | 9.6 | 19.2 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 9.6 | 9.6 | 9.6 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | |
| R8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 9.6 | 0 | |
| R9 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 9.6 | 0 | 0 | 9.6 | 0 | 9.6 | 0 | 0 | |
| R10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 9.6 | 9.6 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.6 | 0 | 0 | 0 | 0 | 0 | |

598 **S2. Contact rates**

599 *Table 3. Significance level for rejection of the null hypothesis that group level average physical*
 600 *contact rates come from identical continuous distributions with equal median under the Wilcoxon*
 601 *rank test. Rates which are not significantly different at the 5% level are highlighted in bold: these are*
 602 *as might be expected assuming lamb-initiated contacts.*

| Flock | Total physical contacts | | p |
|--------------------------------------|-------------------------|-----------------|-------------------------------|
| Ewes with newborn lambs | ewe with ewes | ewe with lambs | $< 10^{-4}$ |
| | ewe with ewes | lamb with ewes | $< 10^{-5}$ |
| | ewe with ewes | lamb with lambs | $< 10^{-5}$ |
| | ewe with lambs | lamb with ewes | < 0.05 |
| | ewe with lambs | lamb with lambs | < 0.66 |
| | lamb with ewes | lamb with lambs | < 0.02 |
| Ewes with nearly weaned lambs | ewe with ewes | ewe with lambs | $< 10^{-3}$ |
| | ewe with ewes | lamb with ewes | $< 10^{-4}$ |
| | ewe with ewes | lamb with lambs | $< 10^{-4}$ |
| | ewe with lambs | lamb with ewes | < 0.05 |
| | ewe with lambs | lamb with lambs | < 0.39 |
| | lamb with ewes | lamb with lambs | < 0.37 |

603

604 Table 4. Significance level for rejection of the null hypothesis that group level average physical
 605 contact rates come from identical continuous distributions with equal median under the Wilcoxon
 606 rank test. All rates between flocks are different with the exception of the contact between ewes
 607 when they have lambs.

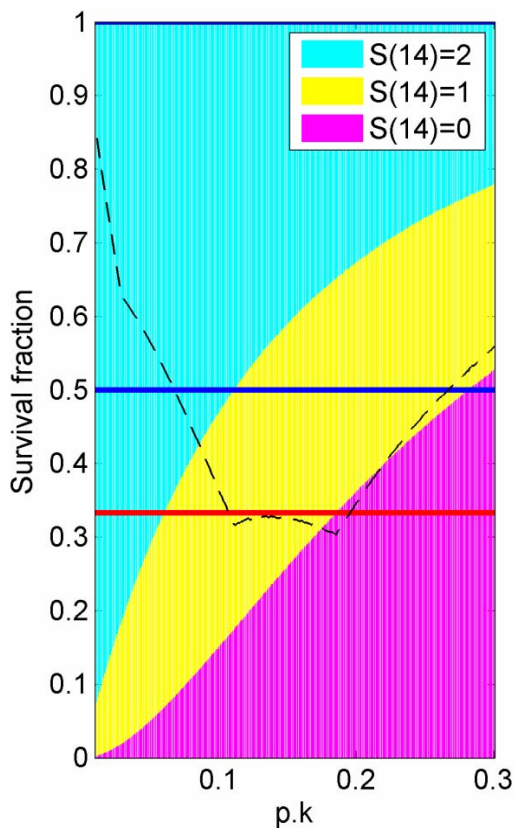
| Physical contacts | Flocks | | p |
|------------------------|-------------------------------|-------------------------------|---------------------|
| | Ewes with newborn lambs | Ewes with nearly weaned lambs | < 0.88 |
| <i>ewe with ewes</i> | Ewes with nearly weaned lambs | Ewes only | < 10 ⁻⁴ |
| | Ewes only | Ewes with newborn lambs | < 10 ⁻⁴ |
| <i>ewe with lambs</i> | Ewes with newborn lambs | Ewes with nearly weaned lambs | < 10 ⁻³ |
| <i>lamb with ewes</i> | Ewes with newborn lambs | Ewes with nearly weaned lambs | < 10 ⁻⁵ |
| <i>lamb with lambs</i> | Ewes with newborn lambs | Ewes with nearly weaned lambs | < 10 ⁻⁵ |
| | Ewes with newborn lambs | Ewes with nearly weaned lambs | < 10 ⁻⁸ |
| <i>any with all</i> | Ewes with nearly weaned lambs | Ewes only | < 10 ⁻⁹ |
| | Ewes only | Ewes with newborn lambs | < 10 ⁻¹⁰ |

608

609 **S3. Disease dynamics**

610 The stochastic single-class ODE model was run with $N = 4$ for $0 \leq pk \leq 1$, with the optimal value
611 (based upon a million replicates) chosen as that which generated a final epidemic size distribution
612 that most closely matched that of the six experiments. Based upon absolute differences (see Figure
613 6) the best fit is given by the product $pk \approx 0.15$. This is similar to the transmission rate $\beta = 0.105$
614 (95% CI: 0.044,0.253) estimated by Orsel et al.(2007).

615 *Figure 6. Shaded regions represent the distribution of the number of uninfected*
616 *individuals expected after 14 days following the protocol of (Orsel et al., 2007), based*
617 *on a million replicates, compared to the proportion of actual experiments in which this*
618 *occurred (horizontal lines). The dashed line is a measure of the discrepancy, based*
619 *upon the absolute difference in all three classes – hence generating two local minima*
620 *(the most appropriate value is considered to be the median of these).*



621

622 Estimates of p require this product to be scaled by a suitable contact rate, which is difficult given
623 the artificial conditions of the experiment. Since the lambs were approximately ten weeks old (Orsel
624 et al., 2007) but separated from their mothers, it is unclear as to whether data for nearly weaned
625 lambs or from non-parental (ewe only) flocks is the most appropriate. Results are presented for the
626 full range of estimated possible p – based upon the highest and lowest contact rates recorded,
627 with the best available estimate considered to be that based on the uniform animal group: $k = 83.3$
628 yields $p = 1.789 \times 10^{-3}$ for FMD in sheep.

629 **S4. Compartmental models**

630 The assumption of the frequency-dependent model is that the total number of contacts an animal
631 has in a given day does not change with flock size; rather, there is a reduction in the average number
632 of contacts between any two individuals as the number of animals increases. This is generally
633 accepted as the most reasonable approximation, especially for larger groups, as it is not expect that
634 animals rush around in a large group maintaining the same number of contacts with all other
635 individuals as they have in a small group, although at present there is no clear data for sheep to
636 confirm this. An alternative formulation is to assume that individuals maintain a certain level of
637 contact between each other, irrespective of the number of animals in the group. The standard
638 (single-class) model then becomes:

$$\begin{aligned} \frac{dS}{dt} &= -pcIS \\ \frac{dI}{dt} &= pcIS - \gamma I \\ \frac{dR}{dt} &= \gamma I \end{aligned}$$

639

640 where c is the average number of contacts per timestep between two individuals (as opposed to k ,
641 the average number of contacts in total that an individual has with all other individuals). This
642 formulation may be more appropriate as the number of animals decreases, since it is unlikely that
643 individuals will try to maintain the same number of total contacts in a small group that they
644 experience in a large group, without some upper limit on the amount of contact between two
645 individuals. It should be remembered, however, that as $N \rightarrow 0$ the underlying assumptions of the
646 compartmental model are undermined, and stochasticity (including die-out) becomes increasingly
647 important. A frequency-dependent formulation is therefore more appropriate for compartmental
648 models.

649 ***S5. Network Analysis Glossary***

650 *Adjacency matrix*: for a network of N individuals, the (i,j) entry of the NxN adjacency matrix indicates
651 how individual i is connected to individual j. If contact is undirected the matrix will be symmetric.

652 *Degree*: the number of connections a given node has to all other nodes. In a weighted network, the
653 weighted degree is the sum of the connection weights.

654 *Dyad*: two individuals regarded as a pair.

655 *Weight*: the strength attached to each link. In an unweighted network all links are represented by
656 either 0 (no contact) or 1 (contact) in the adjacency matrix.

657