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A farm transmission model for Salmonella in pigs, applicable to EU Members States
Abstract

The burden of Salmonella entering pig slaughterhouses across the European Union (EU) is considered a primary food safety concern. In order to assist EU Member States with the development of National Control Plans, we have developed a farm transmission model applicable to all Member States. It is an individual-based stochastic Susceptible-Infected model, that takes into account four different sources of infection of pigs (sows, feed, external contaminants such as rodents and new stock) and various management practices linked to Salmonella transmission/protection (housing, flooring, feed, All-In-All-Out production). A novel development within the model is the assessment of dynamic shedding rates.

1 The results of the model, parameterized for two case study Member States (one high and one low prevalence) suggest that breeding herd prevalence is a strong indicator of slaughter pig prevalence. Until a Member States’ breeding herd prevalence is brought below 10% then the sow will be the dominant source of infection to pigs raised for meat production; below this level of breeding herd prevalence, feed becomes the dominant force of infection. INTRODUCTION

Salmonella infection and transmission in pigs has been widely described in the literature\(^1\text{--}^4\). Several serotypes commonly isolated from pigs in Europe (for example Typhimurium and Enteritidis) are of significance to human health\(^5,\ 6\). Hence, the burden of Salmonella entering pig slaughterhouses across the European Union (EU) is considered a primary food safety concern. Therefore, through EU legislation, the intention of the European Commission was to set targets for each Member State (MS) to reduce the prevalence of Salmonella infection in pigs at slaughter (although the EU has recently decided to achieve reductions through stricter process hygiene controls instead – see Commission Regulation No 217/2014). The targets were to be based on scientific evidence, including information gathered through two baseline surveys of Salmonella prevalence in slaughter and breeding pigs\(^5,\ 7\), a European Food Safety Authority (EFSA) Scientific Opinion\(^8\), a Quantitative Microbiological Risk Assessment (QMRA)\(^9\) and finally cost-benefit analyses for Salmonella control in slaughter and breeding pigs\(^10,\ 11\). The
primary aim of the overall QMRA was to assess the effectiveness of on-farm and abattoir interventions in reducing Salmonella levels in pigs and/or humans, dependent on MS production systems and current prevalence of infection in breeding (sow) and finishing units. The QMRA modelled the full farm-to-consumption pathway, split into a number of modules: Farm, Transport & Lairage, Slaughter & Processing, Preparation & Consumption and Dose-Response \(^9\). In this paper we discuss in detail the farm model, which describes the transmission of Salmonella within pig herds, and which can be used to investigate interventions that may reduce prevalence in pigs at slaughter.

The main aim of the farm model was to i) better understand and describe the introduction and dynamics of Salmonella infection, and how these are affected by the various management practices across the EU, and ii) to assess the differences in the effect of practical on-farm interventions between EU MSs. The aim of identifying the MS-dependent effectiveness of interventions is key and the results of on-farm interventions, and how these affect MS-level slaughter pig prevalence and subsequently human incidence of Salmonella infection, are described in an accompanying paper \(^12\). In this paper we focus on describing the dynamics of infection, and what are the main sources and drivers of infection in different MSs.

Infectious disease transmission models have been developed for a variety of animal diseases, including Salmonella in pigs \(^{13-16}\). Typically the latter models have become more detailed over time and in the case of a recent study the traditional use of “general” transmission parameters was replaced by specifically modelling the environmental transfer of Salmonella via the faecal-oral route \(^{14}\). A transmission parameter is essentially a “black-box”, which describes the force of infection resulting from Salmonella being present in the environment. An estimate of the parameter thus encompasses many different factors, including the resistance of the pig to infection, the level of contamination in the environment and the frequency of contact with that contaminated environment, without explicitly
describing their individual contribution. However, in order to investigate interventions (such as cleaning and disinfection, vaccination etc...) it is necessary to differentiate between those factors that increase/reduce the level of contamination in the environment and those factors that affect the resistance of the pig to infection. In addition, in order to ensure that any model is relevant across EU MSs then the varying management practices across the EU must be considered. We therefore consider differences in environmental transfer caused by management factors (for example flooring or whether pigs are produced on an All-In-All-Out (AIAO) basis). The farm model was designed to be generic and can be parameterised (given relevant and available data) to represent any EU MS. Within the wider QMRA, four case study MSs were chosen (9); in this paper the results from two of these case study MSs are described (one “low-prevalence” MS and one “high-prevalence” MS, as defined by lymph node prevalence as taken from the baseline EFSA slaughter pig survey (5)).

2 METHODS

2.1 Overview of farm transmission model

The farm model is an individual-based stochastic Susceptible-Infected-Susceptible (SIS) model, adapted to take account of i) multiple changing populations, rather than a single closed population, and ii) intermittent shedding of Salmonella. The model is implemented using Monte-Carlo simulation, where each iteration represents production from one farm over a 500 day period, incorporating farrowing, weaning, and grower and finisher production. Over this 500-day cycle of production batches of pigs are sent to slaughter each week. Two outputs are generated for each batch of pigs sent to slaughter (the inputs to the Transport & Lairage module): the prevalence of lymph-node infection and a distribution for the concentration of Salmonella shed within the faeces of infected pigs. Lymph-node infection is the metric of interest as this is the sample type used in the EFSA slaughter pig baseline survey (7); hence we
wish to be able to validate the model results against this robust EU-wide survey, as well as providing relevant predictive model results for the reduction in a MS’s slaughter-age pig prevalence in light of an intervention program.

For each iteration there are a large number of spatial and temporal events that can occur at random, including the seeding of infection into the farm, the response to exposure (in terms of whether or not infection occurs) and subsequently the shedding rate. All farms are set to be Salmonella-negative at the start of an iteration (day 1). There are four assumed sources of infection: sows, feed, wildlife and the introduction of new infected stock. Following initial infection of the herd, which can occur at any time, transmission is described by an individual-based environmental infection model, which tracks i) the shedding and inactivation/movement of Salmonella in the environment and ii) the dose-response of pigs exposed to environmental contamination.

The baseline model was run for 1000 iterations (representing 1000 farms). Management factors (for example flooring, feed type used) were used to define farm types, for which more description is given later. Farm types were allocated proportionally to the 1000 farms to represent the national structure of the pig herd within a particular MS. Hence, it was assumed that summing the predicted number of lymph-node positive pigs over all batches/farms and dividing by the total number of pigs within the batches provided an estimate for the prevalence of lymph-node positive pigs being sent to slaughter (i.e. leaving the farm gate) for a particular MS.

For clarity we define a distinct difference between the use of the terms “sow” and “pig”. Pigs are explicitly defined as those animals which are raised only for slaughter and progress through all the rearing
stages of farrowing, weaning, growing and finishing. Sows are explicitly those animals producing the pigs raised for slaughter (as opposed to breeding sows in multiplier or nucleus herds).

2.2 Management of farms

Large variability in breeding (sow) and slaughter pig prevalence across EU MSs is apparent from two baseline surveys carried out in 2006-8 (7, 5). While some of this variability can be assumed to originate from topography and climate, the majority will result from the types of production systems used by farmers. Management systems and practices for which there was sufficient evidence to show a direct effect on transmission of Salmonella were included. Individual farms within the model are assigned a farm type based on these relevant characteristics. The options modelled are described in Table I.

It was assumed that all slaughter pigs will go through four main stages of rearing: farrowing, weaning, growing and finishing (fattening) and will be moved into specialist accommodation for each stage of rearing (pigs can be transported between farms at the end of weaning if a two-site system is used). Pigs will spend $sa$ days in the farrowing house before being weaned, then $wa$ days in the weaning accommodation, and then $ga$ and $fa$ days in the grower and finishing stages respectively, before being sent to slaughter on a weekly basis at days $t = (1,8,15,\ldots,498)$. There are $n_{pig}$ pigs in pen $j$, $n_{pen}$ pens in room $l$, and $n_{room}$ rooms in a building. At the beginning of the model ($t=1$) each pen/room/building is populated with pigs (except for one farrowing building, which is left empty for cleaning and disinfection for one week). Assuming most large systems will raise pigs using some form of weekly/fortnightly
batching, the model system described in Figure 1 is used. We also assume Figure 1 is applicable to all
MSs (small adjustments to the parameter estimates are possible to reflect a MS more accurately). The
system is flexible, and differences between rearing stage, inside/outside and AIAO/continuous production
are captured via parameter estimation.

For computational efficiency it was also assumed that pig movement is regimented and efficient, such
that the pens containing the individual batch of pigs sent to slaughter at times $t$ are filled immediately
with the group of pigs within the growing house that have reached finishing weight and that group is
replaced by the batch of pigs reaching the required growing weight etc… For slaughter pigs that are
finished on a grower-finisher farm, it is assumed that they were reared on a breeder-weaner farm and
transported to the grower-finisher farm. Transport has been highlighted as a risk factor for Salmonella
transmission between pigs (17), hence transport is included if this farm type is selected. Transport between
farms is assumed to be almost identical to transport between the finishing house and abattoir, hence the
model we use here is largely based on the Transport & Lairage model (18), except it is assumed only one
cohort (batch) is transported at a time.

2.3 Transmission model

2.3.1 Shedding and removal of faeces
Salmonella is primarily transmitted via the faecal-oral route \cite{19, 20} and the probability of infection is dependent on the dose ingested \cite{21}. In order to examine a range of specific interventions (for example vaccination, changing feed type, cleaning) the amount of Salmonella ingested by a pig and the subsequent dose-response relationship must be considered. The methods used in previous models \cite{13, 14} were expanded; in particular shedding and the subsequent movement/ingestion of faecal material. For the rest of this section a general parameter definition is used for all stages of production (farrowing, weaning etc…) unless explicitly stated.

The total amount of faecal material in pen \( j \) of room \( l \) at time \( t \) is defined as \( F(j,t) \). The amount of faecal material shed by an animal, \( k \), during any one timestep (one day) is defined as \( f(k, j, t) \sim N(\mu_f, \sigma_f^2) \) for pigs. Similarly, \( f_{sow}(j, t) \sim N(\mu_s, \sigma_s^2) \) for sows. It is assumed that fresh faeces (i.e. those shed on day \( t \)) will be more viscous than older faeces and will hence be more amenable to fall through slatted flooring. The proportions of faecal material shed on day \( t \) in pen \( j \) of house \( l \) and removed that day via slatted flooring and cross-contamination to an adjacent pen are given by \( \beta_{F,day}(j, t) \) and \( \beta_{xc}(j, t) \) respectively. Regarding faecal material shed prior to day \( t \), that is faecal material present on day \( t-1 \), the proportions removed via slatted flooring and cross-contamination are \( \beta_{F,old}(j, t) \). The amount of faecal material present in pen \( j \) of house \( l \) at the end of day \( t \) is calculated using equations (1) – (4) as follows:

The total amount of faecal material shed by pigs on day \( t \) is

\[
F_{pig}(j,t) = \sum_{k=1}^{n_{pig}} f(k, j, t). \tag{1}
\]

except in the farrowing building where

\[
F_{pig}(j,t) = \sum_{k=1}^{n_{pig}} f(k, j, t) + f_{sow}(j,t)
\]
The amount of faecal material shed on day $t$ removed from pen $j$ is given by

$$F_{\text{day}}(j,t) = F_{\text{pig}}(j,t) \cdot (1 - \beta_{F,\text{day}}(j,t) - \beta_{w}(j,t)).$$

The amount of faecal material shed before day $t$ and removed via slatted flooring on day $t$ is given by

$$F_{\text{old}}(j,t) = F(j,t-1) \cdot \beta_{F,\text{old}}(j,t).$$

The amount of faecal material shed before day $t$ and cross-contaminated to either pen $j-1$ or $j+1$ on day $t$ is given by

$$F_{x}c(j,t) = F(j,t-1) \cdot \beta_{x}c(j,t).$$

Finally,

$$F(j,t) = \begin{cases} 
F(j,t-1) + F_{\text{day}}(j,t) - F_{\text{old}}(j,t) - F_{w}(j,t)/2 + F_{w}(j+1,t)/2 & \text{if } j = 1 \\
F(j,t-1) + F_{\text{day}}(j,t) - F_{\text{old}}(j,t) - F_{w}(j,t)/2 + F_{w}(j+1,t)/2 & \text{if } j = 2, \ldots, n_{\text{pen}} - 1 \\
F(j,t-1) + F_{\text{day}}(j,t) - F_{\text{old}}(j,t) - F_{w}(j,t)/2 + F_{w}(j-1,t)/2 & \text{if } j = n_{\text{pen}} 
\end{cases}$$

The set of pens depopulated through each production stage are assumed to be cleaned out before new pigs are moved in. We assume cleaning out of faecal material at this depopulation time is efficient, therefore $F(j,t) = 0$, for all rooms which are depopulated/re-populated at times $t$. In contrast, it is assumed that Salmonella removal will not be 100% efficient (as Salmonella may be released from the faecal material and reside in biofilms or hard-to-clean areas such as feeder tube nipples).

### 2.3.2 Introduction of Salmonella into pig herd

It was assumed that a pig will be in any one of two states at time $t$; Susceptible or Lymph-node positive (specifically infection in the ileo-caecal lymph node). The concentration of Salmonella shed by Lymph-
node positive pigs is dependent on whether the pig was infected by a “low” (<10^6 CFUs) or “high” (≥10^6 CFUs) dose (which is described in more detail in Section 1.4).

Lymph-node positive status was used to determine infection as it is an ideal characteristic at the point of slaughter for which to validate the model (given the ileo-caecal lymph node was the primary sample type for the EFSA baseline slaughter pig survey \(^{(5)}\)). However, being lymph-node positive does not necessarily mean that the pig will be actively excreting Salmonella. Rather, it is an indication of the fact that the pig still has a Salmonella infection and can potentially shed Salmonella. Therefore, it is important to note that at some timepoints no shedding of Salmonella may occur, even if a pig is lymph-node positive (i.e. “intermittent shedding”). As no data were available, it was assumed that pigs immediately return to the “Susceptible” state following recovery from being lymph-node positive. Recovery from the “Lymph-node positive” state takes \(t_{LN}\) days.

The sources of infection were based on the opinion of EFSA (2006), which are: other infected pigs (sows/new stock/mixing of cohorts), feed and wildlife \(^{(8)}\). The herd prevalence for Salmonella infection in breeding sows, \(p_{\text{herd}}\), was estimated for each MS within the EU from the EFSA breeding survey \(^{(7)}\). At the start of each iteration, infection status of the breeding herd (infected/not infected) is randomly assigned according to the value of \(p_{\text{herd}}\). The within-herd prevalence of Salmonella shedding on breeding herds, \(p_w\), will vary between farms, as well as MSs. The number of sows shedding Salmonella within a batch cohort, \(I\), is binomially distributed according to \(p_w\) and the number of sows within the cohort, \(n_{\text{sow}}\), that is \(I_{\text{sow}}(j,t) \sim \text{Binomial}(n_{\text{sow}}, p_w)\). As each group of piglets reach weaning age the group of sows is replaced with another group of sows reaching parturition, after a week of the pen being empty for cleaning and disinfection (C&D). The number of infected sows in the new group is recalculated using the same process as above.
Each sow will produce $f_{\text{sow}}(j,t)$ faeces per day. If the sow is currently shedding it will excrete Salmonella into the environment at a rate $c_s(j,t)$ (CFUs per gram of faeces). Therefore over a daily period a sow will shed $\lambda(j,t) = f_{\text{sow}}(j,t) \times c_s(j,t)$ salmonellas. Note that sows are treated as a "static" source of infection within the model: they are not infected by either of the other sources considered, or by the shedding of their neighbours. Each sow remains in the same infection state for the duration of farrowing.

For simplicity, it was assumed that feed can be broken down into two major types: wet ($w$) and dry ($d$). Pigs will consume $g$ grams of feed per day and it was assumed that a pig is exposed to a new batch of feed every 4 days. We define the prevalence of feed batch contamination as $p_{\text{feed}}$. The concentration of Salmonella within contaminated feed is denoted as $c_f(k,j,t)$ per gram feed (equal to zero if feed batch is Salmonella-negative). The number of Salmonella ingested per day by a pig, through consumption of contaminated feed is given by $\lambda_f(k,j,t) = g \cdot c_f(k,j,t)$.

There are little data to quantify the frequency and magnitude (and the associated variability over time and between farms) of any external contamination of the farm. However, there are some data on wildlife incursions onto farms and the amount of Salmonella rodents or birds might contaminate the environment with via defecation (22, 23). While recognising other external sources of infection exist, it was decided to incorporate only wildlife (specifically rodents and birds) as a source of infection.

A study into the transmission of Salmonella between wildlife and pigs suggests that wildlife within the vicinity of farms are more commonly infected with Salmonella if the pigs themselves are infected (23). Therefore, it was assumed that the Salmonella status of the wildlife is equivalent to the status of the farm,
i.e. infected or not infected. Rodents and birds are then assumed to contribute $\lambda_e(k,j,t)$ salmonellas to the exposure dose of each pig for each time step onwards from when infection occurs on a farm (assuming, in the absence of any other data, each pig will ingest roughly 1g of rodent/bird faeces per day). Studies have shown that prevalence within rodents/birds on an infected pig farm ($p_{\text{wild}}$) are fairly low, around 1-5% (22, 23). Therefore a Bernoulli random variable (with $p=0.03$) was used to indicate whether a pig would ingest contaminated wildlife faeces such that pig ingestion of Salmonella through external contamination occurs relative to the prevalence of infection within the wildlife. The concentration of Salmonella within wildlife faeces appears to be similar to that within pigs (22). Hence, in the absence of rigorous quantitative data, a lognormal distribution for $\lambda_e(k,j,t)$ was assumed as this is a commonly used distribution to describe microbiological count data (see Table IV).

2.3.3 Transmission of infection via the contaminated environment

Once infection of one or more pigs occurs, transmission between pigs is driven not only by the sources of infection but also by the shedding of contaminated faeces. Observational studies (3, 4, 24) show intermittent shedding by infected pigs at low levels (usually less than 100 CFU/g of faeces) and a fairly low incidence of infection (apart from the period immediately post-weaning, when there is typically a distinct increase in incidence/prevalence). A schematic diagram of this dynamic is shown in the transmission model framework for one pen (relevant to all pens, buildings and stages of production), given in Figure 2.

INSERT FIGURE 2 HERE.
The amount of Salmonella shed into the pen environment each day by each pig ($\gamma(j,t)$) or sow ($\gamma_s(j,t)$) can be given by

$$
\gamma(j,t) = \begin{cases} 
\sum_{k=1}^{n_p} c_p(k,j,t) \cdot f(k,j,t) & \text{if wean, grow or finishing stage} \\
\sum_{k=1}^{n_p} (c_p(k,j,t) \cdot f(k,j,t)) + c_s(j,t) \cdot f_{sow}(j,t) & \text{if farrowing stage}
\end{cases}
$$

where $c_p(k,j,t)$ and $c_s(j,t)$ are the concentrations of Salmonella per gram of faeces shed by a pig and sow respectively ($c_p(k,j,t)$ or $c_s(j,t)$ is zero for susceptible pigs; $c_p(k,j,t)$ and/or $c_s(j,t)$ may also be zero for infected pigs/sows that are intermittently shedding). Similar equations for the total number of Salmonella in the pen environment, as for faecal material (Equations 1-4), can be defined. Therefore,

$$
E_{day}(j,t) = \gamma(j,t) \cdot (1 - \beta_{f,day}(j,t) - \beta_{xc}(j,t)),
$$

$$
E_{old}(j,t) = E(j,t-1) \cdot \beta_{f,old}(j,t),
$$

$$
E_{xc}(j,t) = E(j,t-1) \cdot \beta_{xc}(j,t),
$$

where $E_{old}$ and $E_{xc}$ are the amounts of Salmonella present at day $t-1$ and removed during day $t$ via slatted flooring and cross-contamination respectively. Therefore, the total amount of Salmonella in pen $j$ at the end of day $t$, $E(j,t)$ is given by

$$
E(j,t) = \begin{cases} 
0 & \text{if } j = 1 \\
0 \log(10)(E(j-1)-E_{day}(j,t)-E_{xc}(j,t))/2 + E_{xc}(j-1)/2 & \text{if } j = 2 \ldots n_{pen} - 1 \ (7)
\end{cases}
$$
where $\delta$ is the decay rate of Salmonella (in logs) per day, $t_c$ is the time between depopulation and repopulation (7 days for farrowing, zero days for other stages).

We assume there is imperfect removal of Salmonella during cleaning and/or disinfection. Therefore, for rooms depopulated/repopulated at times $t$, $E(j,t) = E(j,t) \cdot \beta_c$, where $\beta_c \sim \text{Beta}(\alpha, \beta)$ and is the fraction of Salmonella remaining in the pen environment after cleaning.

For simplicity it was assumed that Salmonella is homogeneously mixed within all faecal material in the pen. Therefore the average concentration of Salmonella within a gram of contaminated faecal material, $c$, is given by

$$c(j,t) = \frac{E(j, t)}{F(j,t)}.$$  

### 2.3.4 Infection of pigs

It was assumed that all (Salmonella-negative and positive) pigs ingest some faecal material each day. Therefore, each pig will ingest $\lambda_i(k,j,t)$ organisms through faecal ingestion, where

$$\lambda_i(k,j,t) = \mu \cdot c(j,t)$$

where $\mu$ is a random variable describing the mass of faeces ingested by a pig. The total number of Salmonella ingested by each pig on day $t$, $\lambda(k,j,t)$ can therefore be given as
\[
\lambda(k, j, t) = \hat{\lambda}(k, j, t) + \hat{\lambda}(k, j, t) + \hat{\lambda}(k, j, t).
\]  

(8)

From experimental data \footnote{Experimental data citation}, the probability of a pig becoming infected through ingesting \(\lambda(k, j, t)\) organisms, \(p_{\text{inf}}(k, j, t)\), was shown to follow a beta-binomial dose-response relationship. Hence, at the individual pig level

\[
p_{\text{inf}}(k, j, t) = 1 - \left(1 - \text{Beta}(\alpha_{\text{DR}}, \beta_{\text{DR}})^{\lambda(k, j, t)}\right).
\]  

(9)

where \(\alpha_{\text{DR}}\) and \(\beta_{\text{DR}}\) are the shape and scale parameters of the Beta-Binomial dose response model, and are dependent on feed type. The number of newly infected pigs in pen \(j\), \(e(j, t)\), can therefore be defined as

\[
e(j, t) \sim B(S(j, t), p_{\text{inf}}(k, j, t)).
\]

Each of the newly infected pigs are assigned a duration for being lymph-node positive, \(t_{\text{LN}}\). Hence, at time \(t_{\text{inf}} + t_{\text{LN}}\) (time of infection + duration of infection) a pig will return to the “Susceptible” status (if it has not been transported to slaughter first). We define \(w(j, t)\) to be the sum of infected pigs in pen \(j\) of room \(l\), that have reached the end of their infection period at time \(t\). Therefore, the number of susceptible (\(S(j, t)\)) and infected (\(I(j, t)\)) pigs within a pen at the end of day \(t\) is calculated as follows:

\[
\begin{align*}
I(j, t) &= I(j, t - 1) + e(j, t) - w(j, t) \\
S(j, t) &= n_{\text{pig}} - I(j, t)
\end{align*}
\]
where at $t = 1$ $S(j, t) = n_{\text{pig}}$ and $I(j, t) = 0$. The prevalence of infection within each pen at time $t$, $p(j, t)$ is

$$I(j, t)/n_{\text{pig}}.$$ 

The output of the model is the prevalence of infection (defined as lymph-node positive) within batches of pigs placed on transport to slaughter. Transport to slaughter occurs weekly, i.e. one finishing room (4 pens) from one of the finishing buildings is emptied on each of the movement timesteps $t$ discussed above. The first five batches of pigs sent to slaughter are not included in the results in order to allow sufficient introduction and transmission of infection to occur through the originally Salmonella-free pig population.

Therefore, the prevalence of lymph-node positive pigs at slaughter within a batch of pigs sent to slaughter at times $t$, $p_i(t)$, is given by

$$p_i(t) = \frac{\sum_{j=1}^{4} I(j, t)}{4 \cdot n_{\text{pig}}}. \quad (8)$$

### 2.4 Parameter estimation

There are little or no data to reflect the variation of Salmonella introduction/transmission across EU MSs caused by some of the management factors in terms, and hence for simplicity these parameters were assumed to be equal across all case study MSs (see Table II). The weightings for apportioning farm types were taken from data collected from the EFSA baseline survey for breeding pigs \(^{(7)}\). For farms which the
EFSA baseline survey data did not cover (i.e. farms with no breeding herd) other relevant sources were used (Table III).

All other parameter estimates are detailed in Table IV. The breeding herd prevalence of each case study MS was taken from the EFSA breeding pig survey and assumed to be directly equivalent to $p_{\text{herd}}$. In the absence of data for all case study MSs, it was assumed that, as a worse case scenario, the within-herd prevalence was equal to the MS2 estimate. The prevalence of Salmonella contamination has been identified to be between 1-10% for samples from feed types commonly used for pigs (25). However, there are many issues with sampling of feed for determining prevalence (6). Of concern is the extremely small sample mass (relative to the tonnage produced), meaning that it is highly likely that positive batches are missed if contamination is heterogeneous. Therefore, a conservative estimate of $p_{\text{feed}} = 10\%$ was used for both case study MSs.

Assuming that pigs excrete intermittently during the whole time period of infection (as defined by presence of Salmonella in lymph-node), survival analysis methods were used to estimate the duration of both lymph-node positivity and excretion (26, 3). The resulting shedding profile is highly variable between individual pigs. A recent longitudinal study of outdoor pigs (3) enumerated Salmonella at the individual pig level for six weeks (six weekly samples). Two cohorts of pigs (one high and one low dose group) were seeded with experimentally infected pigs on outdoor paddocks, before these cohorts were removed and two new cohorts placed on the vacated paddocks. There were significantly greater concentrations shed by the high dose group (between 0-10$^6$ CFU/g) than by the low dose group (0-100 CFU/g). Pigs in
the second experiment cohorts were then infected quasi-naturally from the contaminated faecal material shed by the first cohorts. Once a pig has been infected then the magnitude of shedding is randomly assigned from 0 – 6 log CFU/g faeces, according to the dose with which the pig was infected. For every proceeding week after initial infection that a pig remains within the Lymph-node positive state then the magnitude of shedding is determined based on the previous week’s magnitude. On each day an infected pig may shed up to \( x \log \text{CFU/g faeces} \), therefore

\[
\text{if } x > 0, \text{ else } c_p(k,j,t) = 0.
\]

Correlation matrices have been generated from the dataset describing the magnitude of shedding (either 0, 2, 4, 6 log CFU/g faeces) from infected pigs in the second, quasi-naturally infected, cohort, one matrix for each dose group (“low”, 1-10\(^6\) CFU, or “high”, >10\(^6\) CFU). Hence these correlation matrices give the probability of a pig shedding \( x \log \text{CFU/g faeces} \) one week, given it had shed \( y \log \text{CFU/g faeces} \) the previous week.

In order to derive the dose response parameters, \( \alpha_{DR} \) and \( \beta_{DR} \), a Beta-Poisson model was fitted to experimental dose-response data for pigs fed on dry feed (from ileo-caecal lymph-nodes)\(^{21}\). The \( \alpha_{DR} \) and \( \beta_{DR} \) parameters from the Beta-Poisson model are also equivalent to the \( \alpha_{DR} \) and \( \beta_{DR} \) parameters of the Beta-Binomial model. Pigs on wet feed will have a greater resistance to infection, due to the lowering of pH within the gut making it a more hostile environment for Salmonella\(^{27}\). The wet feed parameters were estimated by anchoring the relative change in prevalence between dry and wet-feed farms produced by the model to the relative change in prevalence observed within a German risk factor study using data collected through the EFSA baseline survey for slaughter pigs\(^{28}\).

### 2.5 Sensitivity analysis and model interrogation
An Analysis of variance (ANOVA) method was used for sensitivity analysis \(^{(29)}\). The inputs (or “factors”) were grouped by quartiles and the resultant F-value from ANOVA gives the confidence that a given factor has an effect on the output mean, i.e. the prevalence of infection within a batch of pigs sent to slaughter \(p_i(t)\). Many of the distributions used within the model are sampled many times during one iteration of the model. In order to use the ANOVA method then the mean of the random variable samples drawn from each distribution of one iteration is used to describe the variability between batches. For example the relationship between \(p_i(t)\) and the amount of Salmonella ingested via external contamination, \(\lambda_e(k,j,t)\), is determined by investigating how the value of \(p_i(t)\) is influenced by the mean value of all the individual values of \(\lambda_e(k,j,t)\) drawn from the distribution described in Table III for the relevant pigs \((k)\), pens \((j)\) and building \((l)\).

The relative contribution of each source of infection (sow, feed, external contamination) was investigated by setting, in turn, the contribution of each source to zero. Analysis of individual iterations was used to investigate complex dynamics, such as comparing the distribution of doses ingested against the contamination of the pig environment. Finally, the output was stratified by management factors (for example feed type, flooring type) and by farm type to elucidate any potentially significant differences between farm types.

3 RESULTS

3.1 Baseline results

The average within-batch prevalence of lymph-node positive pigs at slaughter age was estimated to be 0.007 (5th percentile 0, 95th percentile 0.031) for MS1, and 0.176 (0, 0.813) for MS2. The percentage of positive batches for MS1 and MS2 were estimated to be 0.380 and 0.629 respectively. The distribution of
within-batch prevalence (showing only positive batches) is shown in Figure 3. It is clear that most
batches being sent to slaughter are either Salmonella-negative, or infected at a low prevalence. Batches
with a high within-batch prevalence are rarely sent to the slaughterhouse, but it is these high-infection
events that determine the magnitude of the estimated national MS prevalence.

3.2 Sensitivity analysis and model interrogation

The results of the sensitivity analysis are shown in Figure 4. For MS2 the average load of Salmonella
shed by sows is dominant (to the point where the other parameters make little difference). However, for
MS1 feed and external contamination parameters are relatively much more important than the load shed
by the sows (although ultimately the variability associated with the within-batch prevalence is still largely
driven by the average load shed by piglets and weaners within the batch). Further investigation (not
shown) supports the results of the sensitivity analysis; if a sow/pig sheds Salmonella the relative
contribution of the sow/pig to the dose ingested by susceptible pigs is typically much larger than that
contributed by contaminated feed and/or contaminated wildlife faeces.

Figure 5 summarises the impact of each source of infection in determining the slaughter pig prevalence
within the two case study MSs. Within MS2 reducing breeding herd prevalence to zero (i.e. $p_{\text{herd}} = 0$)
removes the vast majority of infections at depopulation; conversely, removing feed or external
contamination as sources does little to change the national pig prevalence. Again, this result suggests that
the sow is a major source of infection; only when sow infection is rare (as in MS1), does feed play an important role in determining slaughter pig prevalence.

Given the above results, further scenario analysis showed that national breeding herd prevalence was strongly correlated with slaughter pig prevalence (in fact, this was the only MS-dependent parameter that had any major bearing on MS slaughter pig prevalence). Caution must be taken when interpreting this result, especially as it is assumed that the strain of Salmonella infecting the sows is the one which infects the pigs all the way through to slaughter (longitudinal studies suggest a much more complex dynamic of competing strain colonisation \(^{(3,4)}\)). However, comparison of breeding and slaughter pig prevalence for each MS from the respective EFSA baseline surveys suggests that there is at least some correlation between slaughter and breeding pig prevalence at a MS level (correlation coefficient 0.457, see Figure 6) \(^{(7,5)}\).

The dynamics which produce the distributions of within-batch prevalence as shown in Figure 3 were also considered by analysing pen contamination rates and the subsequent Salmonella doses ingested by pigs. Comparison of the non-zero doses ingested by pigs on infected farms with the average dose-response curve for Salmonella infection is shown in Figure 7. Infection is, on average, only more likely to occur than not occur (i.e. \(p_{\text{inf}} > 0.5\)) for a very small proportion of exposure events (those above \(10^6\) CFUs). This dynamic corresponds to the results of Figure 3, where the vast majority of batches sent to slaughter are infected at a very low prevalence level.
A novel aspect of this model was the inclusion of a number of farm types, based on the characteristics of the four management factors (feed, flooring, production system, number of sites). Preliminary analysis showed that there were significant confounding factors with the management data (for example within MS2, dry feed was far more common on AIAO farms than on continuous production farms). Therefore, reliable insight can only be generated by observing the results stratified by farm type as a package of management factors (see Figure 8). The significant result is that one management factor, the production system (AIAO versus continuous) dominates the risk by farm type. AIAO production reduces risk to approximately one third of that for continuous production. The impact of other management factors is negligible by comparison.

4 DISCUSSION

The objective of developing the farm model was to describe the dynamics of Salmonella transmission in pigs in sufficient detail to a) differentiate between the dynamics of infection at a MS level, b) investigate the sources of infection and the link, if any, between the breeding herd and infection at slaughter and c) investigate the effect of interventions in reducing slaughter-age prevalence of infection within and between MSs. Objective (c) is ultimately the primary aim of the model and is discussed in depth in an accompanying paper\(^{(12)}\), but the intention is that the mechanistic approach taken here allows investigation of the difference of effect of varying interventions across MSs. This is achieved by allowing the user to
parameterise the model for individual MSs; the inputs of the model will then directly determine the outcome of an intervention via the different interactions between model variables at different parameterisations. For example, an initial condition of the model is the breeding herd prevalence; differences in this input directly influence the effectiveness of different interventions, hence showing that feed interventions are not a priority for those MSs that have breeding herd prevalences greater than around 10%.

In order to meet the objectives of the model, the methodology of previous Salmonella in pig transmission models has been modified and advanced (including modelling of the pig environment in detail) (13, 15, 14). Specifically, we model and parameterise the environmental contamination of pig pens in more explicit detail than previous models (14, 15). We also explicitly include varying management practices (such as feed types and production systems) and the sources of pig infection, which has not been done before. Differentiating between farm types and sources of infection is fundamental in describing the variability between MSs and the current management factors/sources of infection included do mean that the results produced for each MS are very different, according to their particular parameter estimation. As a result of the increased level of modelling detail, the variability between individual pigs, farms and MSs has been captured to a degree not shown before. This is a much needed development, as variation in infection dynamics and management is crucial in determining the end result (i.e. Salmonella infection in slaughter-age pigs) both within and between MSs. The model also allows investigation of specific mechanisms that could be used to intervene and prevent Salmonella transmission in more detail than has been done before.

Exposure to Salmonella, and the response to Salmonella infection in pigs, is incredibly variable, as evidenced by a number of observational and longitudinal studies (3, 4, 30). The model reflects this variability, hence contamination of the pen can vary between 10-10⁹ organisms over short time periods;
such large variation in contamination unsurprisingly leads to large variation in the amount of Salmonella ingested by a pig and subsequently the incidence of Salmonella infection. However, in the majority of situations contamination of the pig environment will result in exposure at a level insufficient to cause infection. It is only in rare cases, where a sow sheds a high level of Salmonella numbers (or rarer still when feed or the environment is contaminated at a very high level) that a high incidence of infection within a batch is predicted. Accordingly, the results of the model suggest that within-batch prevalence is relatively low. It is the relative contribution of highly-infected batches that determine whether a MS has a low or high slaughter pig prevalence.

Management factors applied to each MS are confounded, for example in MS2 dry feed is more likely to be fed on AIAO farms than continuous ones. Hence, analysis of management factors was only possible at a broader farm type level. This analysis (shown in Figure 8) clearly demonstrates that AIAO production is by far the most important risk factor of the management factors considered. Indeed, there were negligible differences between all other farm management factors (for example feed, flooring). It must be pointed out that the AIAO production system assumed in the model is a theoretical description unlikely to be achieved in reality on all but the strictest systems of AIAO production. Of note is that it was not cleaning and disinfection that makes AIAO farms less of a risk, but rather the strict segregation of pigs minimising the opportunity for spread of infection (indeed, cleaning and disinfection has little impact at all in reducing prevalence of infection in slaughter-age pigs\textsuperscript{(12)}).

Piglets are able to become infected while still suckling from their mother, although the evidence is mixed for whether (sero-) positive sows infer maternal immunity to their progeny, hence meaning piglets are less likely to be infected at the point of weaning, or whether seropositive pigs are more likely to shed Salmonella and hence result in a higher likelihood of piglet infection \textsuperscript{(30, 24)}. It is likely that there is a
delicate balance between the strength of immunity and the strength of the burden of infection, which
sometimes results in immunity or infection dependent on the strength of each. Within these studies there
is the indication that infection in piglets could be under-estimated because of a high likelihood of false
negatives. Indeed, the studies referenced were relatively small given the number of animals followed –
there is certainly the probability they simply didn’t sample any highly-infected piglet groups because
these are relatively rare. However, the broad consensus from these studies is that it is not until weaning
(when piglets are faced with the double stresses of being weaned and mixed with other unfamiliar pigs)
that a significant proportion of pigs may become infected with Salmonella. Comparing the model and
these findings, the broad trends are certainly the same as observed in these studies. Infection in piglets is
rare and usually at a low incidence rate. While stress/feed change during weaning is not explicitly
modelled, pigs are mixed together. The larger amount of Salmonella shed by weaners relative to piglets,
and the fact there are more pigs directly exposed to this Salmonella, means that the peak prevalence of
infection is usually observed during the weaning period. There is generally a diminishing prevalence of
infection at the point of slaughter. This agrees with current observational data \(^{(4, 31)}\).

While the model mathematically describes more variability than most equivalent models, not all factors
that describe variability in Salmonella risk in individual slaughter pigs between farms or between MSs
have been included. Indeed, the variability included is limited to the data available for quantitative
modelling. For example, most management factors have been split into dichotomous options: wet/dry
feed, solid/slatted flooring, AI/AO/continuous production. However, in reality the options available for
each factor are multiple and complex. The following potentially important factors have not been included
in the farm model: further differentiation between feed types (for example pelleted versus non-pelleted),
clustering of Salmonella in faeces, varying growth rate (such that pigs are held back in production), and
transmission dynamics between sows. Further differentiation between feed types would have been
difficult to parameterise, but could potentially be important. However the difference in risk between wet/dry feed was assessed to be the largest of all potential feed type combinations, and this difference in risk was negligible when compared to the difference in risk between AIAO and continuous production. Clustering of Salmonella in faecal material has been modelled before \(^{(32)}\), but would also require a more complex model. The effect of clustering in faeces would be to vary (even more so) the daily exposure of pigs to Salmonella, where some pigs would ingest considerably more organisms, and some considerably less. Over the large number of pigs and timesteps it can be hypothesised that the effect of this clustering averages out, but this cannot be stated with certainty. In reality, a varying growth rate of individual pigs means pigs may need to be kept back behind their cohort before reaching the correct weight to be moved into a different stage of production or sent to slaughter. This has not been included because of the difficulty in including any variation in pig group size (computationally pig cohorts are represented as matrices, and matrix manipulation is only possible with identical or compatible matrices). Keeping certain pigs back and allowing more mixing between cohorts would almost certainly increase the spread of infection within the model, as the allowance for contact between cohorts in continuous production systems within the model is one of the greatest upward pressures on prevalence for the prevalence of infection in slaughter pigs.

Important data gaps highlighted by the model development were the (variation in) dose-response of pigs to infection, the movement of faecal material and the amount of Salmonella that might be present in the environment due to feed or other external sources of contamination (rodents, birds etc). However, for all information gathered for this model, the trend was that regardless of the type of data needed, it was unlikely that current observational, experimental, longitudinal or survey data would be sufficient to be confident that all the variability had been accurately captured (for example the amount of Salmonella shed by a sow is based on one study that shows high variation between pigs – but did they capture the entire
range of variation?). Given the importance of the breeding herd in seeding infection through the pig production chain, there is a distinct lack of quantitative information to model this crucial area. Better information on the duration of sow infection, the variance in the shedding rate when infected (and whether this is dependent on pregnancy) and the sources of sow infection would be needed before much more extensive modelling could be done in this area. Hence, as with all models, the results produced must be viewed in conjunction with the simplifying assumptions made, which were necessary both because of the need to reduce the complexity of a highly variable pig production system across the EU and the data gaps that result because of this complex system.

It is difficult to quantitatively validate the current farm transmission model, as quantitative data are scarce. However, qualitatively the farm transmission model appears to agree well with observed data, and replicates a number of important trends observed in the field (for example relationship between breeding herd prevalence and MS-level slaughter pig prevalence, peak and troughs in prevalence at weaning and finishing, extremely variable nature of infection, and the difference between AIAO and continuous production). The results of the combined Farm and Transport & Lairage models for slaughter pig lymph node prevalence in the two case study MSs compared well to the results of the EFSA slaughter pig baseline survey \(^{(5, 18)}\). In summary, given the need to balance potentially myriad risk factors against the need for a parsimonious model that uses reliable data, we are of the opinion that the model provides a useful summary of the variation that is sufficient to describe the relative importance of different risk factors between farms and MSs and provides a strong platform for investigating on-farm interventions.

Another validation approach is to compare our results with recent, similar models. Such a comparison identifies the progressive complexity required to model interventions by incorporating environmental contamination and considering the contact structure of pigs through commercial pig production systems
The result of these previous models is that “super-shedding” sows or pigs are key drivers of infection; as we have found, Berriman et al. (33) also note that cleaning and disinfection is essentially made redundant if there are super-shedding pigs entering the rooms after cleaning. Minimising contact of susceptible pigs with these super-shedding pigs is crucial if spread of infection is to be controlled, hence why AIAO production is the most important management factor in controlling Salmonella. In short, most recent models for Salmonella in pigs are in agreement that explicit consideration of the batch management system and the variability in shedding and/or environmental contamination is absolutely necessary for accurate representation of infection dynamics. The model presented here advances the methodology by including a data-based dose response model for pig infection, as well as incorporating several different farm management practices and three sources of Salmonella infection.

Analysis of the model pointed to one overwhelming conclusion: the level of infection within a MS’s breeding herd largely determines the slaughter pig prevalence for that MS. The analysis showed that if the sow is infected and shedding at high levels, then commonly (although not always) this will mean one or more piglets will become infected: when this occurs then the shedding of Salmonella by infected pigs, at the farrowing stage or later, dominates the risk (as once a slaughter pig is infected, the subsequent shedding of Salmonella more than outweighs the contribution of contamination within the environment provided by feed and/or the external environment). Such a phenomenon is also hypothesised as a major risk factor for cattle “super-shedding” VTEC O157 (35, 36). However, in low prevalence MSs of which MS1 is typical, infection of the sow is relatively rare (such that it is unlikely that a “super-shedder” sow will occur in the 500 days of production modelled) and the proportion of initial infections of a piglet, weaner etc… via either feed or external contamination are relatively much higher. This result of breeding herd prevalence determining slaughter pig prevalence is supported by data from the EFSA Salmonella in pig surveys; breeding herd prevalence was correlated, at least to some degree, with slaughter pig
prevalence \(^{(7,5)}\)(although the low correlation coefficient may be the result of sampling bias/errors, it could also represent variation in MSs that our model has yet to capture). Incoming infected pigs are also considered to be a primary source of infection for weaning and finishing houses \(^{(8)}\). In summary, breeding herd prevalence is likely to be a strong predictor of national pig prevalence for many MSs and feed only becomes an important source of infection once contamination of the environment by sows or other slaughter pigs is reduced to low levels.

5 References


45. Carr, J. Garth Pig Stockmanship Standards. Sheffield: 5m Enterprises; 1998.


47. Leek, ABG, Callan, J.J., Henry, R.W., O'Doherty, J.V. The application of low crude protein wheat-soybean diets to growing and finishing pigs. Irish Journal of Agricultural and Food Research, 2005; 44:247-60.


Table I: Description of management factors included within the farm model.

<table>
<thead>
<tr>
<th>Management factor</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>One site or two-site farm</strong></td>
<td>Two types of farm are considered: farms rearing slaughter pigs from birth to slaughter weight (breeder-finisher) or farms rearing birth to approximately 8 weeks old and then transferring pigs to a specialist finisher site (breeder-weaner and finisher only). These two types are considered sufficient to capture differences in transmission that would occur through transport of pigs during production.</td>
</tr>
<tr>
<td><strong>All-in-all-out versus continuous production</strong></td>
<td>All-in-all-out (AIAO) production has been shown to be a protective factor for Salmonella infection (37, 38). AIAO production as modelled is the theoretical ideal; batches of pigs are kept together in one room for each of the weaning, growing and finishing stages without any direct contact with any other batches all the way through rearing. All other systems are termed “continuous”.</td>
</tr>
<tr>
<td><strong>Indoor versus outdoor production</strong></td>
<td>Outdoor production has become more popular for large-scale production within the last couple of decades. According to data from the EFSA baseline survey for breeding pigs (7) large-scale outside production is still quite rare for pigs beyond the stage of weaning, and therefore only the farrowing stage is included as a possible outside production stage.</td>
</tr>
<tr>
<td><strong>Feed type</strong></td>
<td>Feed can be both a source of Salmonella infection in pigs and a factor in determining the level of transmission. As with management systems, feeding systems are variable between farms. Of particular importance is whether the feed is presented in a dry or wet form, or whether it is pelleted or non-pelleted (39, 40, 43). Only the distinction between wet or dry feed is assumed because there is some information on the relative effect of wet/dry feed on the prevalence of Salmonella infection in pigs and good information on whether a farmer uses wet/dry feed from the EFSA baseline survey for breeding pigs (7).</td>
</tr>
<tr>
<td><strong>Flooring type</strong></td>
<td>While the evidence for flooring type affecting Salmonella transmission is varied (39, 40), logical thinking suggests that properly maintained slatted flooring may well have some effect as it will remove faeces/Salmonella from the pig environment. Again, there are many flooring types (partially slatted, bare concrete, straw-laden), but it is not possible with current data to differentiate between individual types of flooring, and hence only the distinction between slatted and solid flooring is considered.</td>
</tr>
</tbody>
</table>
Table II: Estimates for farm management parameters.

<table>
<thead>
<tr>
<th>Notation</th>
<th>Description</th>
<th>Stage*</th>
<th>Unit</th>
<th>Value (for large and small farms unless otherwise stated)</th>
<th>Comment/reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$n_{pig}$</td>
<td>Number of pigs within a pen</td>
<td>Far</td>
<td>-</td>
<td>11</td>
<td>Far - 1 sow, 10 piglets (41-43)</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td></td>
<td></td>
<td>40</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G</td>
<td></td>
<td></td>
<td>40</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td></td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>$n_{pen}$</td>
<td>Number of pens within a room/building</td>
<td>Far</td>
<td>-</td>
<td>Large 16 Small 10</td>
<td>Assumed</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td></td>
<td></td>
<td>AIAO 4 Cont (Large 16 Small 10)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G</td>
<td></td>
<td></td>
<td>AIAO 4 (Large 24 Small 10)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td></td>
<td>AIAO 4 (Large 24 Small 10)</td>
<td></td>
</tr>
<tr>
<td>$n_{room}$</td>
<td>Number of rooms within a building</td>
<td>Far</td>
<td>-</td>
<td>1</td>
<td>Assumed</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td></td>
<td></td>
<td>Large 4 Small 1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G</td>
<td></td>
<td></td>
<td>Large 6 Small 1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fin</td>
<td></td>
<td></td>
<td>Large 6 (2 buildings) Small 1 (1 building)</td>
<td></td>
</tr>
<tr>
<td>$wa$</td>
<td>Age at weaning</td>
<td>Day</td>
<td></td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>$ga$</td>
<td>Growing period</td>
<td>Day</td>
<td></td>
<td>Large 42 Small 28</td>
<td></td>
</tr>
<tr>
<td>$fa$</td>
<td>Finishing period</td>
<td>Days</td>
<td></td>
<td>Large 84 Small 63</td>
<td></td>
</tr>
</tbody>
</table>
Table III: Structure of case study MS pig populations reflected using the percentage of slaughtered head production that is reared through each farm type (raw data provided from EFSA breeding pig survey (5) and a MS2 research project (31)).

<table>
<thead>
<tr>
<th>Farm type</th>
<th>Case study member state</th>
<th>MS1</th>
<th>MS2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Breeder-Finisher</td>
<td>Breeder-weaner</td>
<td>Finisher only*</td>
</tr>
<tr>
<td>I - A - So - D</td>
<td>0.00%</td>
<td>0.00%</td>
<td>0.00%</td>
</tr>
<tr>
<td>I - A - So - W</td>
<td>3.30%</td>
<td>3.85%</td>
<td>3.30%</td>
</tr>
<tr>
<td>I - A - Sl - D</td>
<td>3.30%</td>
<td>5.13%</td>
<td>3.30%</td>
</tr>
<tr>
<td>I - A - Sl – W</td>
<td>20.88%</td>
<td>28.21%</td>
<td>20.88%</td>
</tr>
<tr>
<td>I – C - So - D</td>
<td>0.00%</td>
<td>0.00%</td>
<td>0.00%</td>
</tr>
<tr>
<td>I – C - So - W</td>
<td>10.99%</td>
<td>7.69%</td>
<td>10.99%</td>
</tr>
<tr>
<td>I – C - Sl - D</td>
<td>1.10%</td>
<td>3.85%</td>
<td>1.10%</td>
</tr>
<tr>
<td>I – C - Sl - W</td>
<td>45.05%</td>
<td>35.90%</td>
<td>60.43%</td>
</tr>
<tr>
<td>O - A - So - D</td>
<td>0.00%</td>
<td>1.28%</td>
<td>0%</td>
</tr>
<tr>
<td>O - A - So - W</td>
<td>1.10%</td>
<td>0.00%</td>
<td>0%</td>
</tr>
<tr>
<td>O - A - Sl - D</td>
<td>0.00%</td>
<td>0.00%</td>
<td>0%</td>
</tr>
<tr>
<td>O - A - Sl – W</td>
<td>5.49%</td>
<td>3.85%</td>
<td>0%</td>
</tr>
<tr>
<td>O – C - So - D</td>
<td>0.00%</td>
<td>0.00%</td>
<td>0%</td>
</tr>
<tr>
<td>O – C - So - W</td>
<td>4.40%</td>
<td>5.13%</td>
<td>0%</td>
</tr>
<tr>
<td>O – C - Sl - D</td>
<td>0.00%</td>
<td>0.00%</td>
<td>0%</td>
</tr>
<tr>
<td>O – C - Sl - W</td>
<td>4.40%</td>
<td>5.13%</td>
<td>0%</td>
</tr>
</tbody>
</table>


* Breeding survey does not include finisher-only farms.

* Breeding survey does not include finisher-only farms; it was assumed that finisher-only farms have same proportions as breeder-finisher farms.

* Given negligible production from outside sources, for simplicity we assume only piglets reared outside; therefore outside production for finisher-only farms set to 0% (remainder added to most common type)
### Table IV: Estimates for parameters relating to Salmonella infection.

<table>
<thead>
<tr>
<th>Notation</th>
<th>Description</th>
<th>Units</th>
<th>Value/Distribution</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p_{herd}$</td>
<td>National prevalence of Salmonella-positive breeding herds</td>
<td>-</td>
<td>MS1: 0.059</td>
<td>(7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>MS2: 0.44</td>
<td></td>
</tr>
<tr>
<td>$p_w$</td>
<td>Prevalence of infection within a breeding herd</td>
<td>-</td>
<td>MS1: 0.21 (MS2)</td>
<td>(7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>MS2: 0.21</td>
<td></td>
</tr>
<tr>
<td>$p_{feed}$</td>
<td>Probability of feed lot contamination</td>
<td>-</td>
<td>0.10</td>
<td>Assumed from (25, 44)</td>
</tr>
<tr>
<td>$f_{sow}(j,t)$</td>
<td>Mass of faeces defecated by sow per day</td>
<td>g</td>
<td>N(3000,150)</td>
<td>(42)</td>
</tr>
<tr>
<td>$g$</td>
<td>Amount of feed consumed per day at stage H:</td>
<td>g</td>
<td>Wean (~6 wks): 500</td>
<td>(35)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Grow (~12 wks): 1620</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Fin (~18 wks): 3200</td>
<td></td>
</tr>
<tr>
<td>$c_s$</td>
<td>Concentration of Salmonella in contaminated sow faeces</td>
<td>CFU/g</td>
<td>LogNormal(2.36,4.39)</td>
<td>(11)</td>
</tr>
<tr>
<td>$c_f$</td>
<td>Concentration of Salmonella in contaminated pig feed</td>
<td>CFU/g</td>
<td>GPareto(0.001,0,1)</td>
<td>(40)</td>
</tr>
<tr>
<td>$\lambda_e$</td>
<td>Concentration of Salmonella in external environment</td>
<td>CFU/g</td>
<td>LogNormal(0.1,3)</td>
<td>(22)</td>
</tr>
<tr>
<td>$f$</td>
<td>Mass of faeces defecated by piglet per day</td>
<td>g</td>
<td>N(100,10)</td>
<td>(45)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>N(753,50)</td>
<td>(47)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>N(1194,50)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>N(2580,50)</td>
<td></td>
</tr>
<tr>
<td>$c_p$</td>
<td>Concentration of Salmonella in contaminated pig faeces</td>
<td>CFU/g</td>
<td>0-10$^6$ CFU/g (see text)</td>
<td>(3)</td>
</tr>
<tr>
<td>$\beta_{F,day}$</td>
<td>Removal coefficient for fresh faeces on slatted flooring</td>
<td>-</td>
<td>Beta(40,10)</td>
<td>Assumed</td>
</tr>
<tr>
<td>$\beta_{F,old}$</td>
<td>Removal coefficient for old faeces on slatted flooring</td>
<td>-</td>
<td>Beta(2,10)</td>
<td>Assumed</td>
</tr>
<tr>
<td>$\beta_c$</td>
<td>Cleaning coefficient for solid flooring</td>
<td>-</td>
<td>Beta(3,2)</td>
<td>Assumed</td>
</tr>
<tr>
<td></td>
<td>Cleaning coefficient for slatted flooring</td>
<td></td>
<td>Beta(1,2)</td>
<td></td>
</tr>
<tr>
<td>$\beta_{xc}$</td>
<td>Cross-contamination coefficient</td>
<td>-</td>
<td>Beta(1,10)</td>
<td>Assumed</td>
</tr>
<tr>
<td>$\delta$</td>
<td>Decay constant</td>
<td>day$^{-1}$</td>
<td>0.04</td>
<td>(48, 49)</td>
</tr>
<tr>
<td>$\mu$</td>
<td>Mass of faeces ingested by piglets per day</td>
<td>g</td>
<td>U(0,21)</td>
<td>(50, 51)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>U(0,100)</td>
<td>Based on (52) and expert opinion</td>
</tr>
<tr>
<td>$a_{DR}, \beta_{DR}$</td>
<td>Parameters of dose response model</td>
<td>-</td>
<td>Wet: $a_{DR}$: 0.1766; $\beta_{DR}$: 50235</td>
<td>(38, 41)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Dry: $a_{DR}$: 0.1766; $\beta_{DR}$: 20235</td>
<td></td>
</tr>
<tr>
<td>$t_{LN}$</td>
<td>Duration of intermittent shedding</td>
<td>days</td>
<td>Weibull(44.94,1.68)</td>
<td>(3)</td>
</tr>
</tbody>
</table>
**Figure 1**: Schematic of pig flow through generic large farm system as modelled. Pigs are reared through 4 distinct stages: farrowing (4 weeks - upon which one batch of pigs from farrowing building is mixed into 1 room of 4 pens in weaner building), weaning (4 weeks), growing (6 weeks) and finishing (12 weeks). Examples of flow are given by shaded annotations: i) single-hatched; piglets are weaned and grouped into batch of 4 pens within one weaner room at the start of Week 1, moved to growing accommodation on Week 5, finishing accommodation on Week 11 and slaughtered on Week 23; ii) double-hatched; new group of sows moved into vacated farrowing building 5 on Week 16; piglets are weaned at start of Week 20 and pass through rooms in subsequent accommodation as they become empty at the time where movement occurs.
Figure 2: Schematic diagram of transmission model. Only the interactions associated with pen(j) are shown. The total faecal material in the pen, $F(j,t)$, is added to each day by Susceptibles ($S(j,t)$), Infecteds ($I(j,t)$) and cross-contamination from other pens ($F_{xc}$) while it is simultaneously reduced each day via cross-contamination ($F_{xc}$) or removal, $F_{old}$. This faecal material contains $E(k,j,t)$ salmonellas, which are added to each day from the infected group via shedding in their faeces and reduced each day as a result of decay, $\delta$, and cross-contamination $E_{xc}$. Pigs ingest $\lambda_i$ organisms per day via the amount in the faeces, $\lambda_f$ via feed and $\lambda_e$ via the environment (and $\lambda_s$, organism from sow faeces if piglets during farrowing). This process results in $e(j,t)$ new infections according to the dose ingested and the dose-response relationship applied.
Figure 3: Distribution of within-batch prevalence at the point of pigs being loaded onto slaughterhouse transport. The majority of batches are either Salmonella-negative or infected at a low prevalence.
Figure 4: Sensitivity analysis for MS2 (high prevalence) and MS1 (low prevalence). The response variable is the prevalence of infection within a batch of pigs being sent to slaughter. Sow – average number of Salmonella shed by sows that gave birth to pigs within batch, Piglet, Weaner, Grower, Finisher – average number of Salmonella shed by piglets, weaners, growers and finisher pigs respectively, Wean feed, Grow feed, Fin feed – average number of Salmonella contaminating feed during weaning, growing and finishing periods of the batch, Ext cont – average external contamination dose ingested by pigs during rearing period of batch. For MSs with high breeding herd prevalence (MS2) the load shed by the sow is the most important parameter in the model, as this provides an initial burden of infection for piglets. If the breeding herd prevalence is low (MS1) then the amount of Salmonella in the feed becomes relatively more important (although the amount of Salmonella shed by piglets is the factor with the largest F value).
Figure 5: Relative impact on national pig prevalence for each MS if each source of infection is set to zero. Baseline (black), breeding herds all negative (dark grey), feed all negative (light grey), no external contamination events (white).
Figure 6: Plot of breeding pig herd prevalence within EU MSs (x-axis) vs slaughter pig prevalence.
Figure 7: Comparison of doses ingested by individual pigs (from all stages of production) (solid line – left hand y axes) against the average probability of infection (using only non-zero doses from the model) (dotted line – right hand y axes). The majority of doses ingested by pigs (from faeces, feed and external contamination) are unlikely to result in infection at the average probability of infection. Note different scales of two y axes.
Figure 8: Stratification of output by farm type (for clarity only MS2 inside breeder-finisher herds shown, however results apply to all types). Only significant management factor is production system; the average prevalence in AIAO farms is around one third of that for continuous farms (~0.03 compared to ~0.1). Other management factors did not have any significant effect.