MODELLING ANIMAL SYSTEMS PAPER

Agent-based modelling of foraging behaviour: the impact of spatial heterogeneity on disease risks from faeces in grazing systems

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SUMMARY

Many of the most pervasive disease challenges to livestock are transmitted via oral contact with faeces (or by faecal–aerosol) and the current paper focuses on how disease risk may depend on: spatial heterogeneity, animal searching behaviour, different grazing systems and faecal deposition patterns including those representative of livestock and a range of wildlife. A spatially explicit agent-based model was developed to describe the impact of empirically observed foraging and avoidance behaviours on the risk of disease presented by investigative and grazing contact with both livestock and wildlife faeces. To highlight the role of spatial heterogeneity on disease risks an analogous deterministic model, which ignores spatial heterogeneity and searching behaviour, was compared with the spatially explicit agent-based model. The models were applied to assess disease risks in temperate grazing systems. The results suggest that spatial heterogeneity is crucial in defining the disease risks to which individuals are exposed even at relatively small scales. Interestingly, however, although sensitive to other aspects of behaviour such as faecal avoidance, it was observed that disease risk is insensitive to search distance for typical domestic livestock restricted to small field plots. In contrast disease risk is highly sensitive to distributions of faecal contamination, in that contacts with highly clumped distributions of wildlife contamination are rare in comparison to those with more dispersed contamination. Finally it is argued that the model is a suitable framework to study the relative inter- and intra-specific disease risks posed to livestock under different realistic management regimes.

INTRODUCTION

Many of the most pervasive disease challenges to livestock are transmitted via the faecal–oral route, from mycobacterial pathogens such as *Mycobacterium avium* subspecies *paratuberculosis* (causative agent of Johne's disease) (Judge *et al.* 2005) to nematode parasite infections such as *Haemonchus*

contortus and *Teladorsagai circumincta* (Hutchings *et al.* 2003). An agent-based model was developed which can be used to assess such disease risks. The model builds on earlier work which primarily addressed issues of resource use efficiency, describing grazing and avoidance behaviour in a spatially explicit context (Marion *et al.* 2005; Swain *et al.* 2007). Those models are based on empirically observed behavioural responses to heterogeneously distributed resources and faecal contamination, namely (i) the selection of tall vegetative swards over short swards (Black & Kenney 1984; Arnold 1987; Bazely & Ensor

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1989; Bazely 1990), or nutrient rich swards over nutrient-poor swards (Bazely 1990; Langvatn & Hanley 1993; Wallis de Vries & Schippers 1994) and (ii) a preference for grazing non-contaminated swards over faecally contaminated swards (Dohi et al. 1991; Hutchings et al. 1998). However, herbivores must make such grazing decisions based on incomplete local information with patch selection based on local visual assessment (e.g. sward height) and patch rejection based on even more localized cues (e.g. olfactory cues associated with faeces). The relative strength of these cues will determine the grazing decisions which in turn determine nutrient intake rates, subsequent sward structure and the efficiency of use of the forage resource. Moreover, the trade-off between faecal avoidance behaviour and the desire to maximize intake also controls the risk of exposure to faecally transmitted disease. The focus in the current paper was on grazing and investigative contacts with faeces, regarded as a potential source of infection, and therefore the results are independent of temporal patterns of infectivity (e.g. differences between micro- and macro-parasites) and specific dose-response relationships. Thus the current results make no quantitative statements about the risks associated with specific diseases, but can be interpreted in the context of a wide range of pathogens.

The agent-based model developed in the current paper is based on discrete state-space Markov processes which provide a general and flexible approach (Marion et al. 2007) both to describing and inferring grazing and avoidance behaviour in managed systems. As noted above, the model builds on earlier work which is now briefly summarized. Marion et al. (2005) focused on resource use efficiency from the point of view of the animal and the resource manager, using a spatially explicit individual-based stochastic model incorporating grazing and avoidance behaviour. The importance of spatial heterogeneity in such systems using both simulation studies and more theoretical analysis based on moment-closure approximation was demonstrated (Whittle 1957; Isham 1991; Keeling 2000; Nasell 2003; Krishnarajah et al. 2005). For example, finding that the optimal stocking density obtained from the spatial stochastic process is markedly different from that obtained using the corresponding non-spatial deterministic model, and furthermore that the maximum intake across the herd obtained is lower when spatial heterogeneity is taken into account. Swain et al. (2007) explored the importance of search distance on resource use efficiency using an extension of this earlier model, and Marion et al. (2007) applied stochastic integration based on Markov chain Monte Carlo methods within a Bayesian framework (see Walker et al. 2006 for an introduction and references) to a related model in order to estimate parameters from detailed behavioural observations obtained from an experiment on

faecal avoidance in cattle described in Swain et al. (2008). In the wider literature Schwinning & Parsons (1999) demonstrate the importance of spatial heterogeneity in grazing systems and Parsons & Dumont (2003) reviewed a range of approaches to the problem highlighting for example the role of more complex behaviours such as learning, memory and social interactions. Parsons et al. (2001) considered problems in scaling up from detailed mechanisms describing foraging and grazing behaviour showing that errors in describing functional responses could lead to substantial errors in predicting intake. Farnsworth & Beecham (1999) considered the impact of a range of foraging behaviours on the distributions of both foragers and resources and find that different foraging strategies can have profound impacts on such spatial patterns. While Yearsley et al. (2002) considered the lifetime trade-off between nutrient intake and harmful effects (e.g. from disease) in an evolutionary context, they assumed a simple foraging model in which individual needs are always met. In the current paper, disease risks associated with nutrient intake were considered in the context of a specific spatially explicit stochastic agent-based model incorporating searching and avoidance behaviours, as described above. To highlight the role of spatial heterogeneity on disease risks from faeces a deterministic equivalent model was also developed, which ignores spatial heterogeneity and searching behaviour, and compared with the spatially explicit agent-based model.

The remainder of the current paper is organized as follows. In Section 2, the stochastic agent-based framework (Marion et al. 2005; Swain et al. 2007) is extended to account for a number of novel features including avoidance of both livestock and wildlife faeces, livestock faecal deposition and disease risk as measured by grazing and investigative contacts with local faecal contamination. In Section 3, the model is parameterized to represent a set-stocking scenario for beef cows in a temperate grassland system, and subsequently used to explore the effect of, and interaction between, search distance and the distribution of faeces, on the risk of exposure to faecal–oral and faecal–aerosol-mediated disease. Disease risks from both wildlife and livestock faeces are considered. In the model, wildlife faeces are not replenished and simply decay in situ (i.e. wildlife are considered to be effectively excluded from the system once cattle are introduced), whereas ongoing deposition and decay of livestock faeces is assumed. In Section 4, the results are discussed and the potential for further developments of the approach is considered. In particular, it is argued that the model represents a suitable tool with which to assess relative levels of risks posed for example by faeces of a range of wildlife species (e.g. rabbits and badgers), compared to those of livestock, or by alternative management practices such as set-stocking or rotational grazing.

DEVELOPMENT OF THE MODEL

The spatially explicit, stochastic agent-based model of Marion *et al.* (2005) and Swain *et al.* (2007) primarily addressed issues relating to resource use efficiency. Novel features introduced are: (i) the introduction of wildlife faecal contamination and associated decay and avoidance parameters; (ii) a model for faecal deposition by livestock; and (iii) measurement of daily grazing and investigative contact rates as indicators of disease risk.

The search component of the current model derives from Swain *et al.* (2007), while the remainder of the model, namely grass growth, intrinsic bite rate and avoidance of livestock faeces, was introduced in Marion *et al.* (2005).

In the current model, the state-space represents, at site i, the sward height h_i, the number of animals c_i, and the contamination f_i due to livestock and w_i due to external sources such as wildlife faeces. In addition s_k represents the stomach contents of animal $k = 1, \dots, N_a$, where the total number of animals is $N_a = \sum_{i=1}^{N} c_i$. All state variables are assumed to be integers. The sward growth rate in each patch, $i = 1, \dots, N$, is assumed to be logistic $\gamma h_i(1 - h_i/h_{\max})$. The grazing rate of each individual animal in patch i at time t, is

$$\beta(h_i(t) - h_0)e^{-\mu_f f_i - \mu_w w_i}, \qquad (1)$$

where β is the per-capita feeding rate, h_0 represents the ungrazeable portion of the sward, and μ_f and μ_w are the avoidance parameters for livestock and wildlife faeces, respectively. When a grazing event occurs the local sward height is reduced, and the stomach contents increased by one unit. The rate of decay of faecal contamination at patch i is $\lambda_w w_i$ for wildlife faeces and $\lambda_f f_i$ for livestock faeces. Individuals are assumed to defecate in their current patch at a rate,

$$f_{\text{dep}}(s_k - s_0)\Theta(s_k - s_0), \qquad (2)$$

where the *Heaviside function* $\Theta(s_k - s_0)$, which is unity if $s_k > s_0$ and is zero otherwise, ensures that individuals deposit s_0 units of faeces per deposition event only if they contain at least s_0 units of forage. This means that intake and livestock faeces are measured in the same units, but the level of faecal contamination is purely notional.

A crucial part of the herbivore foraging process is searching for the specific patch to take a bite. Searching not only includes the movement of the animal through its foraging environment, but also the cognitive and sensory processes to make a foraging decision (Ungar 1996). The range (distance) of view over which a grazing herbivore can detect differences between patches, and so make decisions, will also play a role in the grazing process, and this 'local information' is especially important in more heterogeneous environments. The search distance of

herbivores varies considerably between species, and their circumstances, and is difficult to measure (Phillips 1993), but will be a key factor in determining the level of contact between herbivores and faeces. Thus, it is necessary to test the sensitivity of the model (i.e. in terms of levels of cattle contact with faeces in the environment) to changes in the search distance by varying this parameter within a range expected for example for grazing cattle.

Marion *et al.* (2005) assumed strictly local searching, in which animals can only move to adjacent patches; however, in reality animals may choose to make longer range moves to maximize intake. Therefore, to gauge the potential impact of such wider range searching, strictly local searching was contrasted with global searching in which moves are simulated (at least potentially) across the entire model lattice rather than in a restricted local neighbourhood. The rate at which an animal moves from patch i to patch j is

$$\frac{\nu}{z(i)} F(i, j)h_j(t), \qquad \forall j \in N_i, \qquad (3)$$

where N_i is understood as the entire lattice excluding site i, and ν is the intrinsic search, or movement rate as above. The normalization factor $z(i)$ is given by

$$z(i) = \sum_{j \in N_i} F(i, j) \qquad (4)$$

and, if $|i - j|$ denotes the Euclidean distance between patch i and j, the search kernel follows the power law

$$F(i, j) = |i - j|^{-\alpha}. \qquad (5)$$

The normalization factor $z(i)$ ensures that animals do not get stuck in the corners of the lattice (the boundary conditions are not periodic). In addition, this normalization means that for a large value of the power law search coefficient α (> 10) animals only search nearest neighbouring patches and the movement sub-model reduces to that of the original formulation described above (Marion *et al.* 2005) while for $\alpha = 0$ the animals search uniformly over all patches and the model is closer to the spirit of Schwinning & Parsons (1999). The movement model described by Eqns (3)–(5) was explored in Swain *et al.* (2007) in terms of its effect on sward structure and herbivore intake.

The events and event rates are summarized in Table 1 and subsequently this model is simulated as a stochastic (discrete state-space Markov process) model in which during a given small time interval from t up to $t + \delta t$, written as $(t, t + \delta t)$, an event of type x with associated rate r_x occurs with probability $r_x \delta t$. The total event rate $R = \Sigma_x r_x$ is given by summing the bite, movement and deposition rates in Table 1 across all animals, and the growth and faecal decay rates over all patches. The time-step δt is then

Table 1. *Agent-based model of grazing behaviour defined in terms of the sward height h_i, the number of animals c_i, and wildlife and livestock faecal contamination, respectively w_i and f_i, in patches $i = 1, ..., N$. The sward grows logistically at rate $\gamma h_i(1 - h_i/h_{max})$, and an individual agent – labelled k – currently at patch i takes bites at rate $\beta(h_i - h_0) \exp(-\mu_f f_i - \mu_w w_i)$, movses from patch i to j at rate $\nu F(i, j)h_j/z(i)$, or deposits faeces in patch i at rate $(s_k - s_0) f_{dep} \Theta(s_k - s_0)$. Note that in the deposition rate $\Theta(.)$ is the heaviside function and $\Theta(s_k - s_0)$ is unity if the stomach contents s_k exceeds the size of the faecal deposit s_0, and is zero otherwise. The faecal contamination decays at rates $\lambda_w w_i$ for wildlife faeces and $\lambda_f f_i$ for livestock faeces*

	Change in state space					
Event description	δh_i	$\delta i(k)$	δs_k	w_i	f_i	Event rate at time t
Grass growth at patch i	+1	0	0	0	0	$\gamma h_i(1 - h_i/h_{max})$
Animal k bites at its current location patch $i = i(k)$	−1	0	+1	0	0	$\beta(h_i - h_0)^* \exp(-\mu_f f_i - \mu_w w_i)$
Movement of animal k from current patch $i(k)$ to patch j	0	$i(k) \to j$	0	0	0	$\dfrac{\nu}{z(i)} F(i, j)h_j$
Faecal deposition at current patch $i = i(k)$	0	0	$-s_0$	0	$+s_0$	$(s_k - s_0)f_{dep} \times \Theta(s_k - s_0)$
Decay of wildlife faecal contamination at patch i	0	0	0	−1	0	$\lambda_w w_i$
Decay of livestock faecal contamination at patch i	0	0	0	0	−1	$\lambda_f f_i$

chosen such that $R\delta t < 1$ (i.e. all the terms $r_x \delta t < 1$ can be interpreted as probabilities). For example, see Renshaw (1991) for an introduction to Markov process modelling and simulation of biological populations and Marion *et al.* (2007) for a more detailed description of the above algorithm.

In the appendix, an analogous deterministic and non-spatial model was developed based on the events and corresponding rates shown in Table 1. This model necessarily ignores animal searching behaviour, and comparison of the outputs of this non-spatial model with the agent-based model will highlight the role of spatial heterogeneity, and the partial knowledge of foraging animals, in the system.

Measuring biologically meaningful quantities

Although now defined, an important part of the process of using such a model is the specification of the statistics that should be obtained when running the model. In order to summarize the spatial structure of the system the spatial mean and variance of the sward height were calculated. With sward height h_i at time t and in patch i with $i = 1, ..., N$ patches, the mean sward height

$$\langle h \rangle = \frac{1}{N} \sum_{i=1}^{N} h_i \quad (6)$$

and variance in sward height over all patches at time t

$$var[h] = \frac{1}{N} \sum_{i=1}^{N} h_i^2 - \langle h \rangle^2 \quad (7)$$

can be used to monitor the response of the pasture to grazing pressure. For example as described in Section 3, they are used to enable a set-stocking

regime to be established. In order to model exposure to disease risk from wildlife faeces via the faecal–oral route the daily number of bites taken from patches contaminated with wildlife faeces is recorded, which for day d is

$$\varepsilon o_w(d)$$
$$= \int_{t_d}^{t_{d+1}} \sum_{i=1}^{N} I(\text{bite at site } i \text{ at time } t \,|\, w_i(t) > 0) \, dt, \quad (8)$$

where $I()$ is an indicator function that returns 1 if the statement is true, and day d runs from time t_d to t_{d+1}. Similarly, exposure to disease risk from wildlife faeces via the faecal–aerosol route is measured by the daily number of investigative contacts with (i.e. visits to) patches contaminated with wildlife faeces, which for day d is given by

$$\varepsilon a_w(d)$$
$$= \int_{t_d}^{t_{d+1}} \sum_{i=1}^{N} I(\text{move to site } i \text{ at time } t \,|\, w_i(t) > 0) \, dt. \quad (9)$$

Similar, daily bite $\varepsilon a_f(d)$ and investigation $\varepsilon a_f(d)$ rates are constructed for cattle faeces.

EXPLORING DISEASE RISK VIA THE FAECAL–ORAL AND FAECAL–AEROSOL ROUTES

Parameterization

The model described in Section 2 was parameterized to simulate grazing with three beef cows in a set-stocked temperate grassland system. It was considered
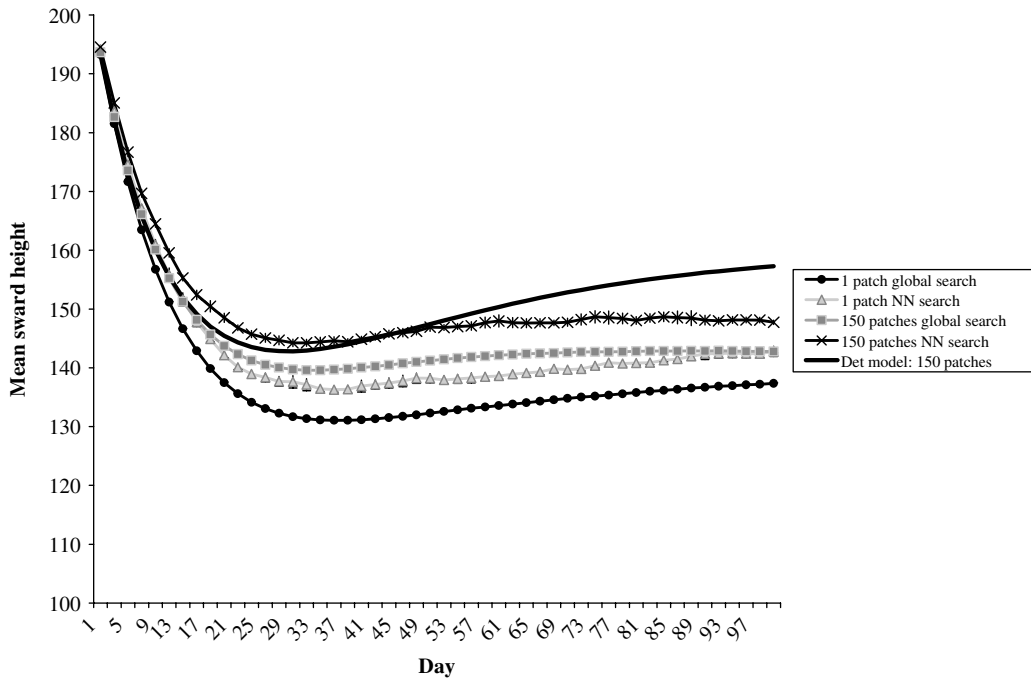
Fig. 1. Mean sward height over all patches for day 1 to 100, estimated from 10 stochastic realizations of the model, with parameter values as described in the text. These results show that the chosen parameters are representative of a set-stocked system with off-take approximately balancing sward growth. The four sets of results shown with symbols relate, as indicated, to different distributions of wildlife faecal contamination (dispersed and clustered) and long- and short-range searching behaviour of the livestock. The solid line shows the deterministic model (see appendix) run with 150 patches of wildlife contamination.

important to ensure the simulations represented the spatial scale of agricultural systems even though the process of disease transmission occurs at the scale of biting. Thus, all simulations were carried out in a 70×70 patch lattice, where each patch represented $0 \cdot 5$ m², the approximate area of one faecal pat and the rejected area around it (Phillips 1993). The lattice of $N = 4900$ patches therefore represented a pasture of $0 \cdot 25$ ha. Model time was measured in min, and all the simulations were run for 100 days. The set stocking parameters $(h_i(0) = 200,\ h_{max} = 400,\ \gamma = 0 \cdot 00004)$, where mean grass height is stable (i.e. sward net growth = herbivore intake), were calculated from herbivore grazing rate parameters (β and h_0) that represented approximately 20 000 bites of herbage a day ($\beta = 0 \cdot 1,\ h_0 = 50$) (Phillips 1993), and a search rate (ν) that represents a cattle step rate of approximately three steps per min (Lazo & Soriguer 1993) ($\nu = 0 \cdot 015$). Numerical simulations (see Fig. 1) confirm that these parameter values give rise to a situation under set stocking where grazing off-take approximately matches sward growth. At the start of the simulation, cattle were introduced into a pasture free of any cattle faecal contamination ($f_i = 0\ \forall$

$I = 1, \ldots,\ N$) and cattle deposited faeces approximately $10–15 \times$/day (Phillips 1993) ($f_{dep} = 1 \cdot 0$, $s_0 = 2000 \cdot 0$). No upper limit on an individual animal's daily intake was set, allowing the animals to graze continuously. Cattle faeces had a decay rate, where complete degradation would occur 3 months after deposition (Haynes & Williams 1993) ($\lambda_f = 0 \cdot 00001776$). Cattle initial avoidance of their own fresh faeces was set at almost complete avoidance (Forbes & Hodgson 1985) ($\mu_f = 0 \cdot 0025$). The parameters relating to wildlife faeces were chosen to represent different scenarios of wildlife faecal distribution as described below.

Defecation patterns and search distance scenarios

The sensitivity of the model to changes in search distance was investigated. Four scenarios were simulated with the same total amount of faeces in the environment (1000 units), with two defecation patterns (one contaminated patch, representative of a concentration of faeces e.g. at a latrine site) *v.* 'dispersed' defecation patterns (150 'contaminated patches') and two search distances (global search distance ($\alpha = 0$)

v. nearest neighbour search distance ($\alpha = 10$)). The avoidance level, μ_w represented the cattle's initial avoidance of a patch of fresh faeces in the environment. The avoidance behaviour intensifies with increasing μ_w and faecal contamination w_i. Thus, in order to keep avoidance of each patch constant regardless of the amount of contamination in the patch, μ_w was varied for each defecation pattern and set to represent extremely high avoidance of each patch i.e. representative of $\mu_w \times w_i(0) = 10$, where $w_i(0)$ represents the initial level of contamination. The wildlife faecal decay rate remained constant for all simulations so that at the end of the simulation (day 100) 0·10 of the initial wildlife faeces remained in the system ($\lambda_w = 0.00001599$).

Measurements of cattle grazing behaviour

As described in Section 3 a range of outputs were measured from each simulation. In particular the mean sward height $\langle h \rangle$ defined in Eqn (6) was reported and, for wildlife (cattle) faecal contamination, the daily bite εo_w (d) (εo_f (d)) and investigation εa_w (d) (εa_f (d)) rates; see Eqns (7) and (8) and surrounding text. Due to the stochastic nature of the model each scenario described above was repeated over 10 randomly realized simulations. Therefore, for each of these output variables the mean was reported (e.g. the mean number of bites/investigations of wildlife faecal contaminated patches per day), averaged over the 10 simulations, and $\pm$ the standard deviation.

The contact rates with livestock faeces did not differ significantly between treatments or runs and therefore these are shown as an average value over all treatments and the standard deviations omitted for the sake of clarity. Where applicable, the corresponding quantities obtained from the non-spatial deterministic model (see appendix) are also presented.

RESULTS

The set-stocked nature of the system parameterized above is illustrated in Fig. 1, which shows the stabilization of the mean sward height over the 100 days of the simulation demonstrating that off-take and sward growth approximately match.

The changing nature of disease risks over the course of the simulation, from both faecal–aerosol and faecal–oral routes of transmission are depicted in Figs 2 and 3, respectively. The former shows the number of investigative contacts made with both livestock and wildlife faeces, while the latter plots the number of bites taken from patches of each contamination type. Figure 4 plots the changing nature of wildlife and livestock faeces in terms of mean levels across all patches and Fig. 5 shows the sward heights for clean patches and for those contaminated with livestock and wildlife faeces. In the case of wildlife faeces, results are presented for the four scenarios described earlier, namely highly clumped and dispersed faecal distributions for both global and local searching.

The investigative contacts with cattle faeces shown in Fig. 2 mirror both the increase in mean cattle faecal contamination levels shown in Fig. 4 and the increase in the number of patches contaminated with cattle faeces (not shown). The decaying levels of wildlife faeces shown in Fig. 4 would therefore suggest that the rate of investigative contacts with wildlife faeces should also fall. However, the initial rise in such contacts, seen in Fig. 2 and note only for dispersed contamination patterns, can be understood with reference to Fig. 5, where the difference in mean sward heights of clean and contaminated patches grows rapidly at the start of the simulation, driving the increased investigation of patches contaminated with wildlife faeces, despite the decay noted earlier. This difference in sward heights between clean and contaminated patches also enhances the increase in investigations of cattle contaminated patches. The decay in levels of wildlife faeces, which in contrast to cattle faeces is not renewed by ongoing defecation, ultimately leads to a fall in the rate of contact for dispersed wildlife faeces (Fig. 2). This effect is reinforced by the eventual decrease in the number of patches contaminated with wildlife faeces (not shown). In contrast to the dispersed cattle and wildlife contamination discussed above, the highly clumped wildlife latrines are investigated extremely rarely. It is also noteworthy that the results are not impacted by the simulated local and global search strategies.

The daily bite rate on contaminated swards (see Fig. 3) reflects risks associated with faecal–oral route transmissions and is driven by both the investigation rate discussed above and by the local sward height. The increase in ingestion of cattle faeces mirrors the increase in mean contamination (Fig. 4) and investigative contacts (Fig. 2) discussed above. The time evolution of bite rates on wildlife contaminated patches is more complex, with an initial rise related to an increased rate of investigation (shown in Fig. 2), and a subsequent fall due to the decaying nature of this faecal contamination (Fig. 4). However, the timing of the peak ingestion rate for wildlife faeces does not correspond to the peak in investigation because the increase in sward height seen in wildlife contaminated patches and the decay of wildlife faeces both increase the bite rate per visit. This also explains why the bite rate on wildlife patches does not fall off as fast as the rate of investigation (Fig. 2). Again, these results for dispersed cattle and wildlife contamination are not impacted by the simulated local and global search strategies, and the highly clumped wildlife latrines are investigated extremely rarely.
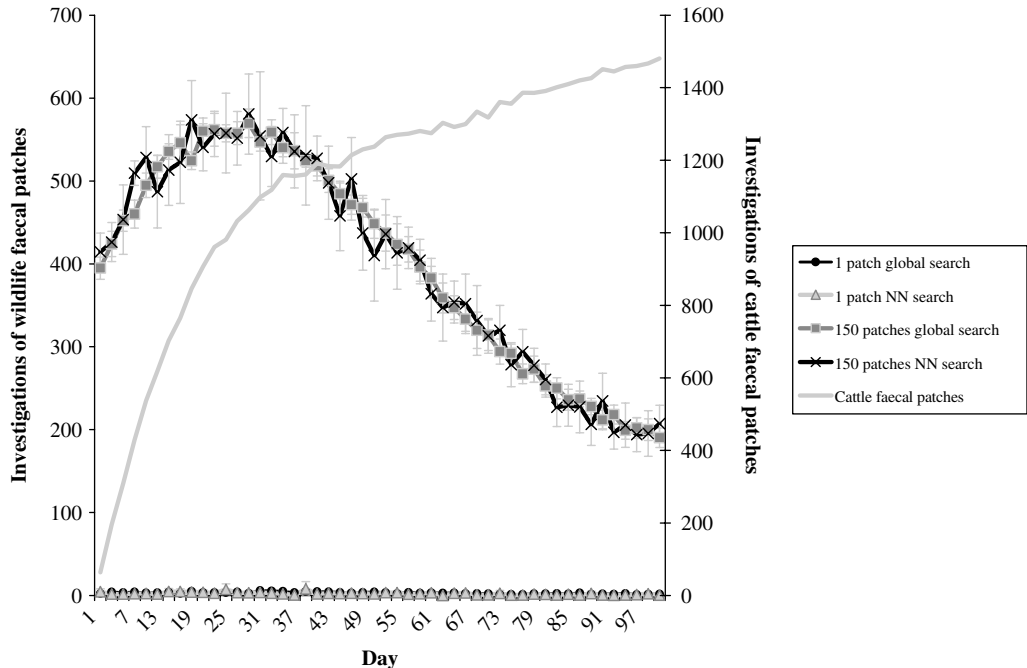
Fig. 2. Effect of wildlife faecal defecation pattern and search distance on the number of investigations taken by cattle from wildlife faecal contaminated patches. One wildlife faecal contaminated patch is representative of latrine type defecation pattern and 150 wildlife faecal contaminated patches is representative of single dispersed deposit defecation patterns. Global search is the grazing herbivore searching all patches in the system at the same rate. NN search is the grazing herbivore searches nearest neighbour patches only. Other parameters as in Fig. 1. Figures are the mean number of bites/number of investigations per day averaged over 10 simulations, ± standard deviation. The daily number of investigations (averaged over all treatments and runs with standard errors omitted) of livestock faecal contamination is also shown (see right-hand scale). The results indicate relative insensitivity to searching ability, but that investigative contact with faeces is strongly determined by its distribution. Note the deterministic model is not shown since it does not account for animal movement.

The results obtained from the non-spatial deterministic model corresponding to the case where the wildlife faeces is spread over 150 patches are also shown on each graph, except for the investigative contacts since movement is not considered in the deterministic approximation (see appendix). The overall sward height (Fig. 1) is slightly over-estimated, and Fig. 5 shows that this results from an under-estimation of the sward height from clean pastures and a corresponding over-estimation of the sward heights in the wildlife and livestock contaminated patches; note that the deterministic model does not account for a higher visit rate to tall swards since search behaviour is not represented. The deterministic representation of the exponential decay of wildlife faecal contamination is essentially exact as expected, but the mean level of livestock faeces is also surprisingly accurate, although latterly this is underestimated (Fig. 4). However, in terms of the level of grazing contacts (Fig. 3) the non-spatial deterministic model is somewhat at odds with the spatially explicit agent-based model. In comparison with the

agent-based model the level of faecal–oral risk from livestock faeces is underestimated (as reflected in the sward height of livestock contaminated pasture). In contrast the risk from ingestion of wildlife faeces is initially underestimated and subsequently over-estimated. In addition the contact rate with wildlife faeces predicted by the deterministic model increases throughout the simulation and the decline seen at around day 70 in the stochastic agent-based model is seen much later (beyond the 100 days shown in Fig. 3) in the deterministic model.

DISCUSSION

In the current paper a spatially explicit agent-based model was developed to describe the impact of foraging and avoidance behaviour on the risk of disease presented by investigative and grazing contact with both livestock and wildlife faeces. The aim was to explore the disease risk exposure resulting from a generic model which captures key aspects of foraging behaviour, namely: searching for desirable patches,
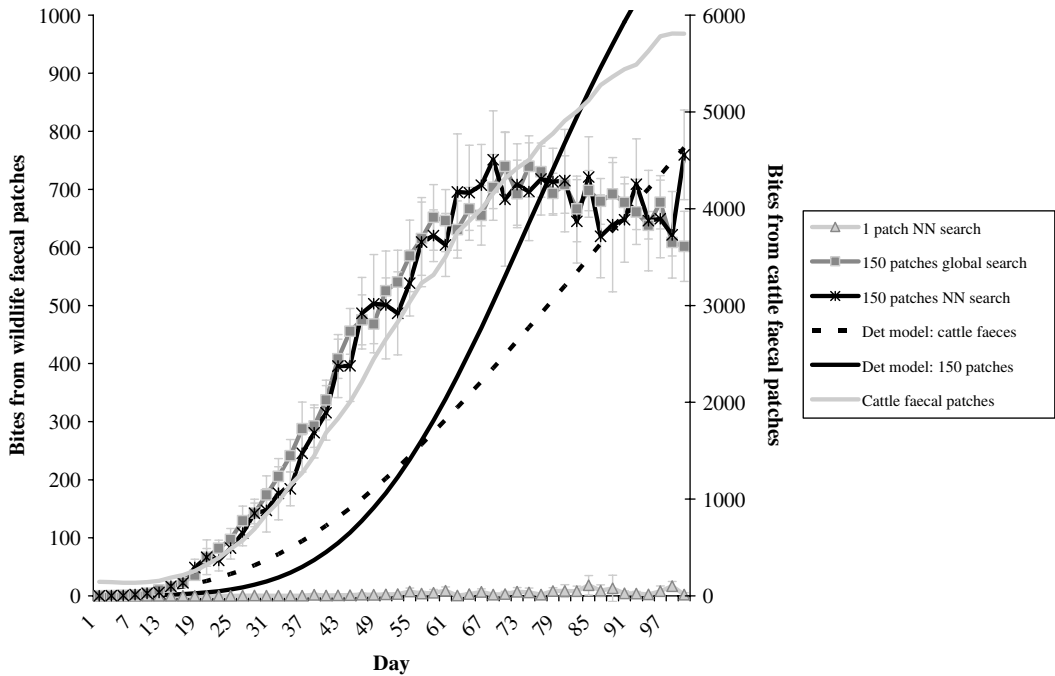
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on the basis of, e.g. their height, and rejection of patches, based on a perception of their level of, e.g. faecal contamination. However, it is worth noting that in reality the searching behaviour of herbivores is more complex than represented in the model. For example, Edwards *et al.* (1997) demonstrated that sheep can form (learn) flexible associations between cues and food resources, while Edwards *et al.* (1996) found evidence of their use of spatial memory. The impact on disease risks of accounting for these more realistic behaviours remains a topic for further research. Nonetheless the relatively simple characterization of herbivore behaviour described in the current paper was sufficient to provide key insights into the nature of disease risks from faecal contamination. To highlight the role of spatial heterogeneity on disease risk, an analogous non-spatial deterministic model, in which neither movement of foragers nor spatial variation in sward height was modelled, was compared with the spatially explicit agent-based model. The current results suggest that spatial heterogeneity is crucial in defining the disease risks to which individuals are exposed, even in the relatively small-scale systems studied.

The models presented in the current paper were parameterized using information from the literature to represent set-stocked beef cows in a temperate grassland system and simulations used to explore model behaviour for the first 100 days during which the system approaches equilibrium in terms of sward growth and off-take. The system was initialized with wildlife faecal contamination which subsequently decayed, but was not replenished. This could be considered realistic if the wildlife in question was effectively excluded from the pasture after restocking, but in any case presented a useful contrast to the role of cattle faeces for which the pasture was initially clean, but was subsequently contaminated by ongoing faecal deposition, despite the decay of individual faecal pats.
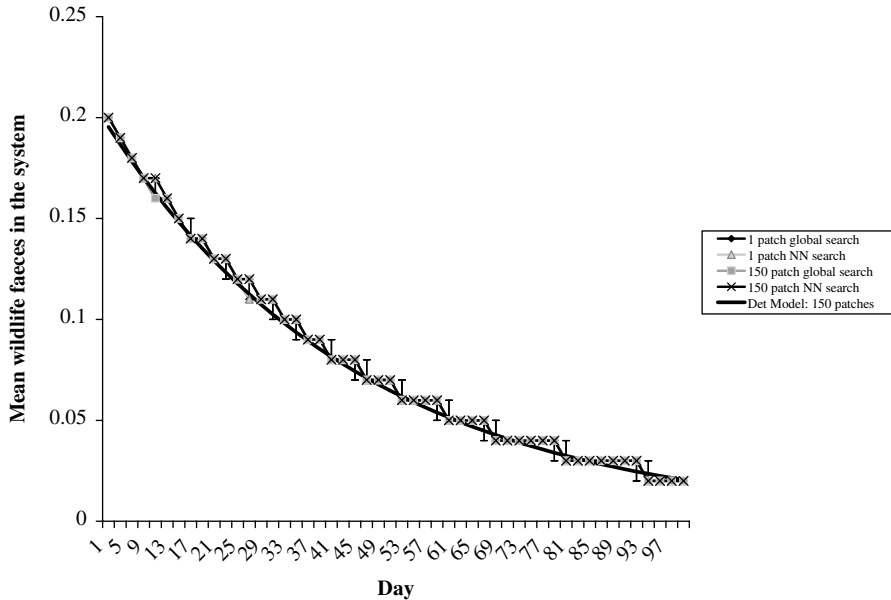
Fig. 4. Average faecal contamination levels for livestock (upper graph) and wildlife (lower graph) contaminated patches. Parameter values as in Fig. 1. The four sets of results shown with symbols relate to different distributions of wildlife faecal contamination (dispersed and clustered) and long- and short-range searching behaviour of the livestock, as indicated. The results show the rise of livestock faecal contamination from the time the animals first enter the paddock and the concomitant decay of the wildlife faeces. The solid lines show the results from the deterministic model (see appendix) run with 150 patches of wildlife contamination.

In terms of disease risk daily bite rates on, and investigative contact rates with, contaminated patches were considered. It is worth noting that, although in most cases disease risk is via a faecal–oral route, disease transmission may also result simply from investigation of contaminated patches via aerosol inhalation which is more likely where faeces and urine are deposited together, for example from *Mycobacterium bovis* in badger urine (Gallagher & Horwill 1977) at badger latrines (Hutchings & Harris 1997). In this context, wildlife contamination in the model could represent badger latrines where avoidance is caused by faecal contamination, while disease risk from investigative contacts arises from urine. As noted earlier, there was no explicit account for the time varying nature of any such disease risk. The current results show that, while both faecal–oral and faecal–aerosol route transmission risks associated with livestock faeces increased over the time frame of the simulations, that associated with wildlife faeces rose and then fell. Moreover, for investigative contacts this pattern was interpreted in terms of sward height differentials between clean and contaminated pasture and the level of faecal contamination. For faecal–oral route disease transmission (i.e. daily bite rate on contaminated swards) the timing of the peak risk was later than the peak investigation rate because

initially faecal avoidance suppresses the bite rate, but latterly avoidance is reduced both by the decay of faeces and the increase in sward height in contaminated pasture.

The current results also suggest that highly clumped wildlife latrines are investigated extremely rarely relative to more dispersed contaminant distributions, in this case including cattle faeces since cattle latrining behaviour was not modelled. However, it is important to emphasize that whether or not latrines pose a risk is dependent on the dose-response curves for disease transmission for the particular disease of concern. In cases where small levels of exposure are relatively likely to result in disease transmission then the current results would suggest that the major risk would come from dispersed faecal distributions. However when a large dose is necessary for transmission of disease then latrines would play a major role.

The simulations presented in the current paper also investigated the impact of herbivore search distance on contact behaviour with different defecation patterns. Swain *et al.* (2007) modelled the effect of various search distances on sward heterogeneity and demonstrated that increased search distance had the greatest impact on taller patches, i.e. increased search distance enabled the animal to identify the tallest
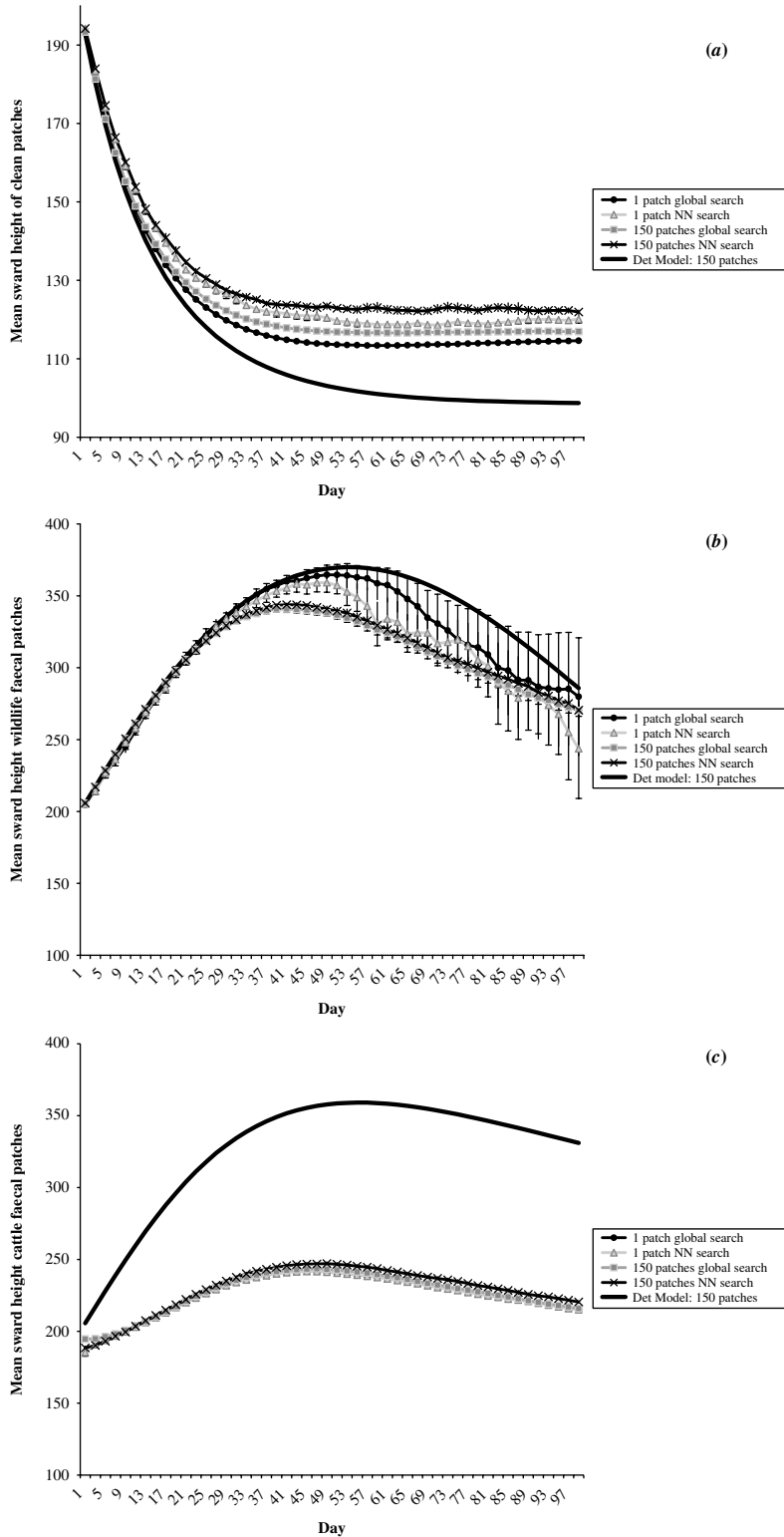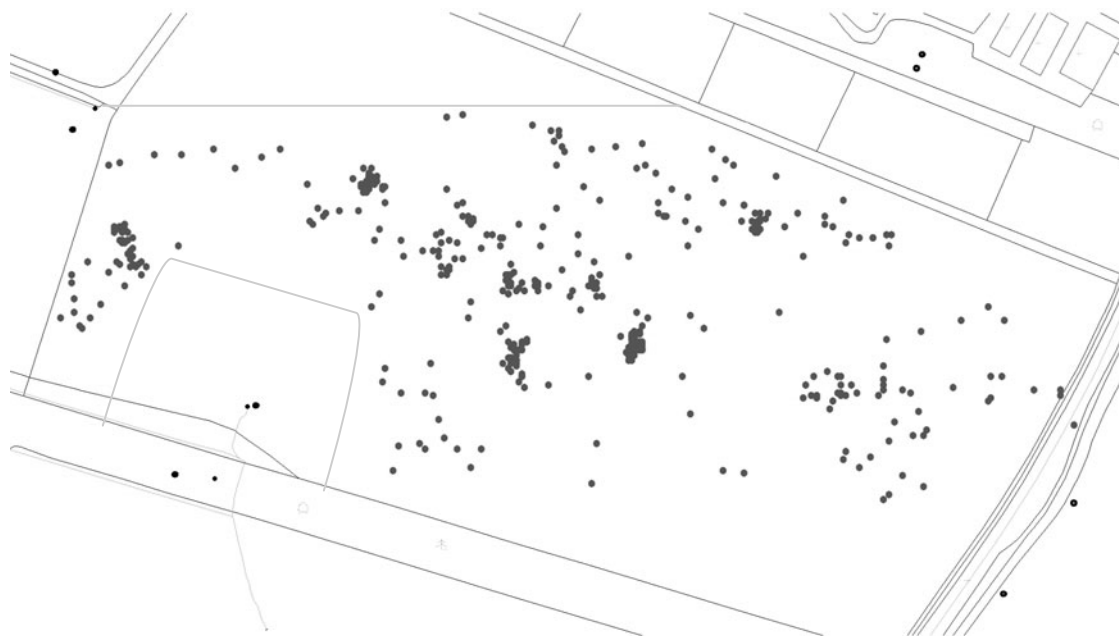
Fig. 5. See opposite page for legend.

Fig. 6. Map of field locations for a single beef cow over a 24 h period (field size = 6·2 ha, herd size = 40 animals) obtained from a Global Positioning System location with an interval of 3 min. The 24 h activity pattern for the animal was chosen at random from an ongoing ITI Scotland Ltd research (see acknowledgements).

patch (in a local neighbourhood) and immediately move to graze it. This suggests that in the simulations presented in the current paper, increased search distance should result in cattle identifying the taller faecally contaminated patches and then moving towards these patches. This would then result in investigation of the patch and rejection of a faecally contaminated patch, leaving a tall sward that remains attractive for grazing. Thus, it might be expected that a global search distance would result in increased investigative contacts compared to nearest neighbour search distance. However, results of the current simulations (Figs 2 and 3) show no difference in contact rates between nearest neighbour and global search distances for both highly dispersed and latrine-type defecation patterns. This effect is likely to be due to the search rate v, i.e. the rate of movement of the cattle in

the system. The model was parameterized to simulate a realistic cattle movement rate of approximately three steps per min (Lazo & Soriguer 1993). This activity pattern is consistent with field studies of cattle movement patterns in Scottish agricultural grazing systems where animals range over the vast majority of a field area on a daily basis, an example of which are the GPS fixes obtained over a 24 h period shown in Fig. 6. Domestic livestock are typically restricted to small field plots in many current agricultural systems and therefore, given such movement rates, even with just nearest neighbour searching might be expected to *consider* a relatively large proportion of patches per day. If contaminated areas are avoided they will become relatively taller over time and therefore the extent to which taller patches are more attractive further increases the chance that contaminated

Fig. 5. Mean sward height in clean patches (*a*) and those contaminated with wildlife (*b*) and livestock (*c*) faeces. Parameter values as in Fig. 1. In each graph, the four sets of results shown with symbols relate to different distributions of wildlife faecal contamination (dispersed and clustered) and long- and short-range searching behaviour of the livestock, as indicated. The results illustrate that the animals preferentially consume clean swards, while sward heights in contaminated patches increase. Subsequent reduction in contaminated sward heights is due to decay of contamination (B – wildlife faeces) and increased trade-off in sward height with clean patches (C – livestock faeces). In each case, the solid lines show the results from the deterministic model (see appendix) run with 150 patches of wildlife contamination.

patches will be contacted. In this context, therefore, it is not surprising that search distance has relatively little impact on exposure to disease risk. Despite the current lack of knowledge of herbivore search distance, these simulations suggest that the movement rate of cattle in pasture is a more important factor in determining transmission risk for faecally mediated disease. This known movement rate results in a high probability of cattle contacting any faeces/parasites in small pastures and thus has important implications for the spread of disease in intensive agricultural systems.

The current paper introduced a modelling framework suitable for the exploration of disease risk to livestock from faecal–oral and faecal–aerosol routes of transmission in a managed agricultural environment. The simulations presented were designed to illustrate the behaviour of the model and the current results demonstrate: (i) the importance of spatial heterogeneity in determining disease risks from faecal contamination; (ii) the relative insensitivity of these results to search distance at least for domestic livestock that are typically restricted to small field plots in many current agricultural systems; and (iii) that contacts with highly clumped distributions of wildlife contamination are rare in comparison to those with more dispersed contamination.

The results suggest that the network of between animal contacts induced by indirect faecal contact is highly connected and therefore that the resulting risk of disease outbreak could be considerably reduced if this indirect contact network was less dense, as is likely to be the case in more extensive systems. It is worth commenting therefore that search distance may become more important in highly extensive settings such as hill grazing and dry systems, where it may also be necessary to account for other behavioural traits such as learning and memory. The model presented here could also be extended to account for other factors such as individual daily intake requirement, and then used to explore the consequences of different management regimes, such as set-stocking and various intensities of rotational grazing, or the relative importance of disease risks posed by inter- and intra-specific faecal contamination for more realistic scenarios than that considered here. However, these and other extensions remain the subject of future work.

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APPENDIX: A NON-SPATIAL DETERMINISTIC MODEL

The model introduced in the main text, and summarized in Table 1, is a spatially explicit individual-based stochastic model described as a continuous-time discrete state-space Markov process. However, in this appendix a non-spatial and deterministic description of this model was constructed based on the rates shown in Table 1. Note that in the deterministic representation the rate of change corresponds to the event rate multiplied by the change in the quantity of interest associated with the event in question. The resulting differential equations can be thought of as a first-order approximation of the underlying spatially explicit stochastic model. A similar approach was taken by Marion *et al.* (2005) who also developed second-order moment-closure approximations which partially accounted for spatial heterogeneity. However, here it has been restricted to the first-order approximation since the discrepancy between this and the full stochastic model measures the importance of spatial correlations and stochasticity in the system.

Efforts were made to construct equations describing the mean sward heights h_c in clean patches, and h_w and h_f in patches contaminated by wildlife and livestock faeces, respectively. As noted above the focus was on mean-field, or first-order approximations, which ignore stochasticity and correlations and are independent of the animal movement model. The mean sward heights in each patch change at rates described in Table 1; increasing according to logistic growth and decreasing at the bite event-rate. The net rates of change of sward height in each patch type are as follows:

$$\frac{dh_c}{dt} = \gamma h_c(1 - h_c/h_{max}) - \beta c(h_c - h_0)$$

$$\frac{dh_w}{dt} = \gamma h_w(1 - h_w/h_{max}) - \beta c(h_w - h_0)e^{-\mu_w w/n_w},$$

$$\frac{dh_f}{dt} = \gamma h_f(1 - h_f/h_{max}) - \beta c(h_f - h_0)e^{-\mu_f f/n_f}.$$

Note that in each case the growth and bite rates depend on the mean sward height in each patch type (i.e. clean, wildlife and livestock contaminated patches), and the average livestock density $c = N_a/N$. In addition the bite rate is reduced according to the contamination level in each patch. It was decided to represent the *overall* level of faecal contamination from wildlife, w, and livestock, f, and the number of patches contaminated with wildlife n_w and livestock faeces n_f, respectively. Therefore the average contamination per plot used in the above equations is w/n_w and f/n_f for wildlife and livestock faecal contamination, respectively.

Since the ongoing deposition of wildlife faeces was not modelled the overall reservoir w decays exponentially,

$$\frac{\mathrm{d}w}{\mathrm{d}t} = -\lambda_w w.$$

Livestock faeces also decay at an exponential rate, but this is offset by faecal deposition of livestock (note the deposition rate is the rate shown in Table 1 multiplied by the size of the faecal deposit)

$$\frac{\mathrm{d}f}{\mathrm{d}t} = -\lambda_f f + (s - s_0)s_0 N_a f_{\mathrm{dep}}\Theta(s - s_0).$$

Similarly, the number of livestock patches increases according to the deposition rate, but it was assumed that the location of patches was assigned at random, which correspondingly reduces the rate as n_f increases towards the total number of patches N.

$$\frac{\mathrm{d}n_f}{\mathrm{d}t} = (s - s_0)N_a f_{\mathrm{dep}}\Theta(s - s_0) \times \left(1 - \frac{n_f}{N}\right).$$

Finally, the deposition rate itself depends on the average stomach contents per animal s which increases according to the total bite rate per animal across all patch types, and decreases according to the faecal deposition rate:

$$\frac{\mathrm{d}s}{\mathrm{d}t} =$$
$$\left[\frac{n_c\beta c(h_c - h_0) + n_w\beta c(h_w - h_0)e^{-\mu_w w/n_w} + n_f\beta c(h_f - h_0)e^{-\mu_f f/n_f}}{N_a}\right]$$
$$- (s - s_0)s_0 f_{\mathrm{dep}}\Theta(s - s_0).$$

These equations are solved numerically and the results contrasted with the stochastic, spatial individual-based model as described in the main text.

In this deterministic approximation, the bite rates $\beta c(h_w - h_0)e^{-\mu_w w/n_w}$ and $\beta c(h_f - h_0)e^{-w_f f/n_f}$ measure the exposure to risks from wildlife and livestock faecal contamination, respectively. In the main text (see Section 3), these are compared with the corresponding risks predicted by the stochastic, spatially explicit agent-based model (summarized in Table 1).