

Understanding the impact of foraging behaviour on disease risks from faeces in spatially heterogeneous systems.

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Abstract

Herbivores have incomplete knowledge of their local environment which creates a two stage grazing process within heterogeneous systems i.e. patch selection based on visual cues (e.g. sward height) and patch rejection based on more localized cues (e.g. olfactory cues associated with faeces). The relative strength of these cues will determine the grazing decisions (i.e. patch choice) of herbivores which will determine their nutrient intake rate, subsequent sward structure and thus the efficiency of use of the forage resource. In addition, the trade-off between faecal avoidance and the desire to maximise intake will control the risk of exposure to faecally transmitted disease. Building on previous work we further develop an agent-based modelling framework used to describe grazing and avoidance behaviour in a spatially explicit context. The framework is based on discrete state-space Markov processes which provide general and flexible methods both to describe and infer the behaviour of a broad range of systems. We explore potential disease transmission risks from both grazing contacts and investigative behaviour, and discuss their relative timing and importance. In addition we explore the impact of different distributions of contamination on disease exposure and explore the sensitivity of such risks to assumptions about the distance over which the animals search.

1. Introduction

Behavioural selection in grazing animals is in part determined by physiological requirements which set energy or nutrient demands of the animal that, in turn result in a strategic behavioural response to the local perception of heterogeneously distributed resources. This behavioural response can be captured by using a series of simple rules which herbivores use when making grazing decisions in heterogeneous landscapes: (i) Select tall vegetative swards over short swards (Black and Kenney, 1984; Arnold, 1987; Bazely and Ensor, 1989; Bazely, 1990); (ii) Select nutrient rich swards over nutrient poor swards (Bazely, 1990; Langvatn and Hanley, 1993; WallisdeVries and Schippers, 1994); and (iii) select non-contaminated swards over faecally contaminated swards (Dohi et al., 1991; Hutchings et al., 1998). However, herbivores have incomplete knowledge of the local environment which creates a two stage grazing process within heterogeneous environments i.e. patch selection based on visual cues (e.g. sward height) and patch rejection based on more localized cues (e.g. olfactory cues associated with faeces). The relative strength of these cues will determine the grazing decisions (i.e. patch choice) of herbivores which will determine their nutrient intake rate, subsequent sward structure and thus the efficiency of use of the forage resource. In addition, the trade-off between faecal avoidance and the desire to maximise intake will control the risk of exposure to faecally transmitted disease. 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 *Teladorsagia circumcincta* (Hutchings et al. 2003), and therefore in this paper we focus on disease risk to livestock from faecal contacts. Building on previous work we further develop an agent-based modelling framework used to describe grazing and avoidance behaviour in a spatially explicit context. The framework is based on discrete state-space Markov processes and we argue that it provides a general and flexible approach both to describing and inferring grazing and avoidance behaviour in managed systems (see Marion *et al.*, 2007). The basic model is extended to represent a range of searching behaviours and spatially explicit environmental pools of (e.g. faecal) contamination.

The remainder of this paper is organised as follows. Section 2 describes the modelling framework used in this paper. A basic model is formulated, and both the importance of spatial heterogeneity, and the estimation of parameters from partial sets of behavioural data are discussed. In section 3 we further develop the model introduced in Section 2 by including longer distance searching behaviour, and environmental patterns of faecal contamination and thus disease risk. In Section 4 this model is then used to explore the interaction between search distance and the distribution of faeces, on the risk of exposure to faecal-oral and faecal-aerosol mediated disease. In section 5 we discuss the results and consider the potential for further developments of this framework.

2. Modelling grazing behaviour in a spatially heterogeneous environment

Marion *et al.* (2005) develop a simple stochastic agent-based model describing the grazing behaviour of herbivores in a spatially heterogeneous environment. The model reflects the biology in that decisions to move to a new location are based on visual assessment of the sward height (or some other proxy for nutritional value) in a surrounding neighbourhood, whilst the decision to graze the current location are based on the residual sward height (or nutritional value) and olfactory assessment of local faecal contamination. The model divides space into N discrete patches with c_i animals and sward height h_i in each patch $i=1, \dots, N$, assumed to be discrete. The agents (animals) either graze the current patch at rate $\beta c_i (h_i - h_0)$ or move to one of z neighbouring patches j at rate $\nu c_i h_j / z$. In addition, the sward growth in each patch, $i=1, \dots, N$, is assumed to be logistic $\gamma h_i (1 - h_i / h_{max})$. The model is summarised in Table 3, which can either be used as the basis for a deterministic model (see below) or 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 is the sum of all event rates, $R = \sum_x r_x$, and the time-step δt is chosen such that the total event probability is less than unity $R \delta t < 1$ (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.

Event description	Change in state space			Event Rate at time t
	δh_i	δc_i	δc_j	
Grass growth at patch i	$+1$	0	0	$\gamma h_i (1 - h_i / h_{max})$
Animal bite at patch i	-1	0	0	$\beta c_i (h_i - h_0)$
Movement of animal from patch i to a neighbouring patch j	0	-1	$+1$	$\frac{\nu}{z} c_i h_j$

Table 1: Agent-based model of grazing behaviour defined in terms of the sward height h_i and the number of animals c_i at patch $i=1, \dots, N$. The sward grows logistically at rate $\gamma h_i (1 - h_i / h_{max})$, and the agents take bites from patch i at rate $\beta c_i (h_i - h_0)$ and move from patch i to j at rate $\nu c_i h_j / z$.

Spatial heterogeneity

Marion *et al.* (2005) show how to construct equations describing spatial averages (i.e. averages over all patches) $\langle f \rangle = \frac{1}{N} \sum_{i=1}^N f(h_i, c_i)$ of functions $f(c_i, h_j)$ of the state variables

for sward height h_j and animal density c_i . For example, note that since there are no births and deaths the animal density $\langle c(t) \rangle$ is constant, and the equation describing the

average sward height $\langle h(t) \rangle = \frac{1}{N} \sum_{i=1}^N h_i(t)$ is written

$$\begin{aligned} \frac{dE[\langle h(t) \rangle]}{dt} = & \gamma \left(E[\langle h(t) \rangle] - \frac{E[\langle h(t) \rangle]^2}{h_{\max}} \right) - \beta E[\langle c(t) \rangle] (E[\langle h(t) \rangle] - h_0) \\ & - \frac{\gamma}{h_{\max}} \text{Var}[h(t)] - \beta \text{Cov}[c(t), h(t)] \end{aligned}$$

where variance in sward height $\text{Var}[h(t)] = E[\langle h^2(t) \rangle] - E[\langle h(t) \rangle]^2$ measures spatial heterogeneity and the covariance $\text{Cov}[c(t), h(t)] = E[\langle c(t)h(t) \rangle] - E[\langle c(t) \rangle]E[\langle h(t) \rangle]$ measures the strength of association between tall swards and the grazing animals. Evolution equations for second-order quantities $\text{Var}[c(t)]$, $\text{Var}[h(t)]$ and $\text{Cov}[c(t), h(t)]$, depend on third-order spatial moments and also on correlations between nearest neighbours. As is typical for such non-linear stochastic processes no analytic solution is currently available, but Marion *et al.* (2005) show how to approximate these equations using moment-closure techniques based on the log-normal distribution. However, in this paper we will focus on simulation results in exploring model behaviour.

Nonetheless the above equation provides valuable insight, for example it involves no approximation and the first line represents the equivalent non-spatial deterministic model which could be formed directly from the sward growth and bite rates in Table 3. The variance and covariance terms in the second line therefore measure the importance of stochastic and spatial effects in the system; if both terms are close to zero then these effects are negligible, but typically they are not and the behaviour of the stochastic and spatial model departs from the non-spatial deterministic analogue in important respects. For example, Marion *et al.* (2005) show that the optimal stocking density obtained from the spatial stochastic process is markedly different from that obtained from the non-spatial deterministic model, and the maximum average intake $\beta \langle c(h - h_0) \rangle$ across the herd obtained is lower when spatial heterogeneity is taken into account. The log-normal approximation partially captures this reduction in intake, but fails to predict the correct optimal stocking density. Marion *et al.* (2005) also introduce additional features and discuss various other aspects of the behaviour of the system including the relative efficiencies of random and directed searching, and the impact of faecal avoidance in the spatially explicit context.

Parameter inference

The modelling approach described above not only accounts for stochastic effects, but also allows parameter inference from incomplete data as described in Marion *et al.* (2007). Partial movement data was available from behavioural experiments described in Friend *et al.* (2002) (see also Swain *et al.*, 2007). A data-logging system composed of transponders worn by the animals and aerials buried under patches of faecally contaminated pasture produced a record of every visit to the contaminated areas for each animal for the four day duration of the experiment. These data were supplemented by the daily measurement of the sward height in the contaminated zones and at a sample of points across the uncontaminated region. The model described above is modified by neglecting sward growth and adding a component describing avoidance behaviour in which the level of faecal contamination of patch i is represented by the variable $f_i \geq 0$ and avoidance modelled by modifying the bite rate to be $\beta c_i (h_i - h_0) e^{-\mu f_i}$. Relative to the case of no avoidance the bite rate is progressively reduced as both the avoidance parameter $\mu \geq 0$ and the level of contamination increase. 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 this model in order to estimate the avoidance parameter, μ and the bite and movement rates, β and ν from the described data set.

3. Extending the model

For our present purposes the model state-space is expanded to represent, 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 $k=1, \dots, N_a$. All state variables are assumed to be integers, and of course $N_a = \sum_{i=1}^N c_i$. The grazing rate of each individual animal in patch i at time t , is

$$\beta (h_i(t) - h_0) e^{-\mu f_i - \mu_w w_i} \quad (1)$$

where as above β is the per-capita feeding rate, h_0 represents the ungrazable portion of the sward, and μ is the faecal avoidance parameter for livestock faeces. The avoidance parameter for wildlife faeces μ_w has a similar interpretation to the livestock faeces avoidance parameter. When a grazing event occurs the local sward height is reduced, and the stomach contents increased by one unit. Sward growth remains unchanged from that described in Table 1. 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,

$$f_{dep} \Theta(s_k - s_0) \quad (2)$$

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 faeces are measured in the same units, but the level of faecal contamination is purely notional.

Searching is now simulated (at least potentially) across the entire lattice rather than in the restricted local neighbourhood described earlier. The rate at which an animal moves from patch i to patch j being

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

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

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

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

$$F(i, j) = |i - j|^{-s} \quad (5)$$

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 normalisation means that for a large value of the power-law search coefficient s (>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) whilst for $s=0$ the animals search uniformly over all patches and the model is closer to the spirit of Schwinning and Parsons (1999). The movement model described by equations (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 for the reformulated model are summarised in Table 2. In the remainder of this paper we study this process as a discrete state-space Markov process in which the event probabilities and simulation algorithm are as defined in section 2.

Event description	Change in state space					Event Rate at time t
	δh_i	$\delta i(k)$	δs_k	w_i	f_i	
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	$\beta(h_i - h_0)^* \exp(-\mu f_i - \mu_w w_i)$
Movement of animal k from current patch $i(k)$ to patch j	0	$i(k) \rightarrow j$	0	0	0	$\frac{v}{z(i)} F(i, j) c_i h_j$
Faecal deposition at current patch $i=i(k)$	0	0	- s_0	0	+ s_0	$f_{dep} \Theta(s_k - s_0)$
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	$\lambda_f f_i$

Table 2: 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 $i=1, \dots, N$. 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 $\beta(h_i - h_0)^* \exp(-\mu f_i - \mu_w w_i)$, moves from patch i to j at rate $vF(i, j)h_j/z(i)$, or deposits faeces in patch i at rate $f_{dep} \Theta(s_k - s_0)$. Note that in the deposition rate $\Theta(\cdot)$ 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.

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 summarise 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 $i = 1, \dots, N$ 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

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

can be used to monitor the response of the pasture to grazing pressure. For example as described in Section 4, 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

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

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

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

Similar, daily bite $\varepsilon_{a_f}(d)$ and investigation $\varepsilon_{o_f}(d)$ rates are constructed for cattle faeces.

4. Exploring disease risk via the faecal-oral and faecal-aerosol routes

Parameterisation

The model described in section 3 was parameterised to simulate a grazing scenario with 3 beef cows in a set-stocking scenario. It was considered important to ensure the simulations replicated the spatial scale of agricultural systems as disease transmission occurs on a bite by bite scale. Thus, all simulations were carried out in a 70 x 70 patch lattice, where each patch represented 0.5m², 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 0.25-ha. Model time was measured in minutes, and all the simulations were run for 100 days. The set stocking parameters ($h_i(0)=200$, $h_{\max}=400$, $\gamma=0.00004$) where mean grass height is stable (i.e. sward growth = herbivore intake) were calculated from a herbivore grazing rate (β) that represented approximately 30000 bites of herbage a day ($\beta = 0.1$) (Phillips, 1993), and a search rate (ν) that represents a cattle step rate of approximately 3 steps a min (Lazo and Soriguer, 1993) ($\nu = 0.015$). Numerical simulations (see Figure 1) confirm that these parameter values give rise to a set-stocked scenario, 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 ($f_i=0 \forall i=1, \dots, N$) and cattle deposited faeces approximately 10-15x a day (Phillips, 1993) ($f_{dep} = 1.0$, $s_0=2000.0$). 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 and Williams, 1993) ($\lambda_f = 0.00001776$). Cattle initial avoidance of their own fresh faeces was set at almost complete avoidance (Forbes and Hodgson, 1985) ($\mu=5$). The parameters relating to wildlife faeces were chosen to represent different scenarios of wildlife faecal distribution as described below (see *Defecation patterns and search distance*). Additionally, insight is gained by contrasting disease risks presented by decaying levels of wildlife faeces with those posed by cattle faecal contamination, which although decaying is also replenished by defecation.

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). Therefore, the maximum distance which a grazing herbivore can search within their environment will also play a role in the grazing process, and especially so in more heterogeneous environments. The search distance of herbivores is currently unknown and extremely difficult to measure (Phillips, 1993), however it may be a key factor in the determining levels of contact between herbivores and faeces in the environment. Thus, it is necessary to test the sensitivity of the model (i.e. levels of cattle contact with faeces in the environment) to changes in the search distance parameter in order to fully parameterise the model to simulate a cattle grazing scenario.

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 (1 contaminated patch, representative of a concentration of faeces e.g. at a latrine site) versus ‘dispersed’ defecation patterns (150 ‘contaminated patches’) and two search distances (global search distance ($s=0$) versus nearest neighbour search distance ($s=10$)). 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 $\mu_w = 10$ for a fixed level of contamination. The wildlife faecal decay rate remained constant for all simulations so that at the end of the simulation (day 100) 10% of the initial wildlife faeces remained in the system ($\lambda_w=0.00001599$).

Measurements of cattle grazing behaviour

As described in section 3 we measured a range of outputs from each simulation. In particular here we report on the mean sward height $\langle h \rangle$ defined in equation (6), and for wildlife (cattle) faecal contamination, the daily bite $\epsilon o_w(d)$ ($\epsilon o_f(d)$) and investigation $\epsilon a_w(d)$ ($\epsilon a_f(d)$) rates; see equations (7 & 8) and surrounding text. Due to the stochastic nature of the model each scenario described above was repeated over 10 randomly realised simulations. Therefore, for each of these output variables we report the mean, (e.g. the mean number of bites/investigations of wildlife faecal contaminated patches per day), averaged over the 10 simulations, and +/- the standard deviation

Results

The set-stocked nature of the system parameterised above is illustrated in Figure 1 which shows the stabilisation 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 Figures 2 & 3 respectively. The former shows the number of investigative contacts made with both livestock and wildlife faeces, whilst 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 Figure 5 shows the sward heights for clean patches and for those contaminated with livestock and wildlife faeces.

The investigative contacts with cattle faeces shown in Figure 2 mirror both the increase in mean cattle faecal contamination levels shown in Figure 4, and the increase in the number of patches contaminated with cattle faeces (not shown). The decaying levels of wildlife faeces shown in Figure 4 would therefore suggest that we should see the rate of investigative contacts with wildlife faeces also fall. However, the initial rise in such contacts, seen in Figure 2 and note only for dispersed contamination patterns, can be understood with reference to Figure 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 (Figure 2). And 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 contacted 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 Figure 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 (Figure 4) and investigative contacts (Figure 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 Figure 2), and a subsequent fall due to the decaying nature of this faecal contamination (Figure 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 (Figure 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 contacted extremely rarely.

5. Discussion

In this paper we have developed a model to describe the impact of foraging and avoidance behaviour on the risk of disease presented by contact with both livestock and wildlife faeces. The model was parameterised to represent a set-stocked system and simulations used to explore model behaviour for the first 100 days during which the system reaches equilibrium in terms of sward growth and off-take. The system was initialised 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, 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 faecal deposition. Moreover this contamination is maintained via ongoing faecal deposition by cattle, despite the decay of individual faecal pats.

In terms of disease risk we considered daily bite rates on, and investigative contact rates with, contaminated patches. 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 (Gallager & Horwill, 1977) at badger latrines (Hutchings & Harris, 1997). Our results show that whilst 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.

Our results also suggest that the highly clumped wildlife latrines are contacted extremely rarely relative to more dispersed contaminant distributions, including cattle faeces since cattle latrining behaviour was not simulated. However, it is important to emphasise 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 our results would suggest that the major risk would come from the dispersed faecal distributions. However when a large dose is necessary for transmission of disease then latrines would play a major role.

The simulations presented here also investigated the impact of herbivore search distance on its 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 patch and immediately move to graze it. This suggests that in the simulations presented here, increased search distance should result in cattle identifying the taller faecally contaminated patches, and then moving towards these patches. The two stage grazing process 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 would be expected that a global search distance would result in increased investigative contacts compared to nearest neighbour search distance. However, results of the simulations here (Figures 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 parameterised to simulate a realistic cattle movement rate of approximately 3 steps per minute (Lazo and Soriguer, 1993). At this movement rate in agricultural systems, it might be expected that cattle are capable of covering the entire pasture each day and therefore grazing is spread evenly across the system. This activity pattern is consistent with field studies of cattle movement patterns in Scottish agricultural grazing systems (Figure 6) where animals range over the vast majority of a field area on a daily basis. Therefore even with nearest neighbour search distances the cattle will move around the field and locate tall wildlife faecal contaminated patches, thus resulting in similar contact rates as cattle with global search distances. 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 increased probability of cattle contacting any faeces/parasites in small pastures, and thus has implications for the spread of disease in intensive agricultural systems. The results presented here suggest that the network of between animal contacts induced by indirect faecal contact is highly connected, however 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 system. It is worth commenting therefore that search distance may become more important in highly extensive settings such as hill grazing and dry systems, and it may also be necessary to account for other behavioural traits such as learning and memory. However, these aspects remain as subjects for further research.

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References

Arnold, G.E., 1987. Influence of the biomass, botanical composition and sward height of annual pastures on foraging behaviour of sheep. *Journal of Applied Ecology* **24**, 759–772.

Bao, J., Giller, P.S., Stakelum, G., 1998. Selective grazing by dairy cows in the presence of dung and the defoliation of tall grass dung patches. *Science* **66**, 65–73.

Bazely, D.R., 1990. Rules and cues used by sheep foraging in monocultures. In: Hughes, R.N. (Ed.), *Behavioural Mechanisms of Food Selection*. Springer, London, pp. 343–367.

Bazely, D.R., Ensor, C.V., 1989. Discrimination learning in sheep with cues varying in brightness and hue. *Applied Animal Behaviour Science* **23**, 293–299.

Black, J.L., Kenney, P.A., 1984. Factors affecting diet selection by sheep. ii height and density of pasture. *Australian Journal of Agricultural Research* **35**, 565–578.

Dohi, H., Yamada, A., Entsu, S., 1991. Cattle feeding deterrents emitted from cattle faeces. *Journal of Chemical Ecology* **17**, 1197–1203.

Forbes TDA, Hodgson J, 1985. The Reaction of Grazing Sheep and Cattle to the Presence of Dung from the Same or the Other Species. *Grass and Forage Science* **40**,177-182.

Gallagher, J. & Horwill, D. M. (1977) Selective Oleic-Acid Albumin Agar Medium for Cultivation of Mycobacterium-Bovis. *Journal of Hygiene* **79**, pp. 155-160

Haynes RJ, Williams PH, 1993. Nutrient cycling and Soil Fertility in the Grazed Pasture Ecosystem. *Advances in Agronomy* **49**:119-199.

Hutchings, M.R., Athanasiadou, S., Kyriazakis, I. & Gordon, I.J. (2003). Can animals use foraging behaviour to combat parasites? *Proceedings of the Nutrition Society* **62**, 361-370.

Hutchings, M.R., and Harris S., 1997. Effects of farm management practices on cattle grazing behaviour and the potential for transmission of bovine tuberculosis from badgers to cattle. *Veterinary Journal* **153** (2): 149-162

- Hutchings, M.R., Kyriazakis, I., Anderson, D.H., Gordon, I.J., Coop, R.L., 1998. Behavioural strategies used by parasitized and nonparasitised sheep to avoid ingestion of gastrointestinal nematodes. *Animal Science*. **67**, 97–106.
- Judge, J., Greig, A., Kyriazakis, I. & Hutchings, M.R. (2005). Ingestion of faeces by grazing herbivores – risk of inter-species disease transmission. *Agriculture Ecosystems and Environment*, **107**, 267-274.
- Langvatn, R., Hanley, T.A., 1993. Feeding patch choice by red deer in relation to foraging efficiency. *Oecologia* **95**, 164–170.
- Lazo A, Soriguer RC, 1993. Size-Biased Foraging Behavior in Feral Cattle. *Applied Animal Behaviour Science* **36**,99-110.
- Marion, G., Walker, D.M., Cook, A., Swain, D.L., & Hutchings, M.R. (2007). Towards an integrated approach to stochastic process-based modelling: with applications to animal behaviour and spatial temporal spread. In: *Redesigning Animal Agriculture* (Ed. by Swain, D. L., Charmley, E., Steel, J. & Coffey, S.): CAB International In press.
- Phillips CJC, 1993. *Cattle Behaviour*. Ipswich, United Kingdom: Farming Press Books.
- Renshaw, E. (1991) *Modelling Biological Populations in Space and Time*, Cambridge University Press, Cambridge.
- Schwinning, S., Parsons, A.J., 1999. The stability of grazing systems revisited: spatial models and the role of heterogeneity. *Functional Ecology* **13**, 737–747.
- Swain, D.L., Hutchings M.R., Marion G, 2007. Using a spatially explicit model to understand the impact of search rate and search distance on spatial heterogeneity within a herbivore grazing system. *Ecological Modelling* **203**, 319–326.
- Swain, D.L., Friend, M.A., Mayes, R.W., Wilson, L.A. and Hutchings M.R. (2007) Combining an active transponder system with sprayed n-alkanes to quantify investigative and ingestive grazing behaviour of dairy cattle in pastures treated with slurry. *Applied Animal Behaviour Science*. In press, doi:10.1016/j.applanim.2007.01.012
- Unger ED, 1996. Ingestive Behaviour. In: *The Ecology and Management of Grazing Systems* (Hodgson J, ed). Wallingford, UK: CAB International; 185-218.
- Wallisdevries, M.F., Schippers, P., 1994. Foraging in a landscape mosaic: selection for energy and minerals in free ranging cattle. *Oecologia* **100**, 107–117.

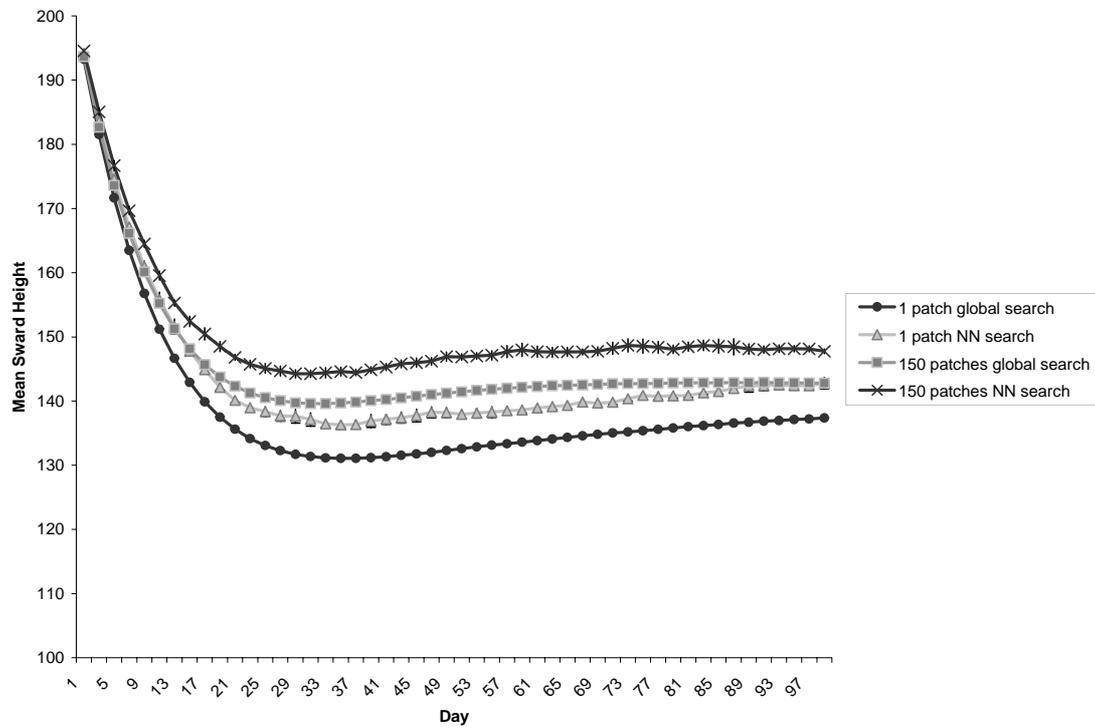


Figure 1: Mean Sward height over all patches for day 1 to 100, estimated from 10 stochastic realisations of the model, with parameter values as described in the text. These results show that the chosen parameters are representative of a set-stocked system with off-take approximately balancing sward growth. The four sets of results relate, as indicated, to different distributions of wildlife faecal contamination (dispersed and clustered) and long and short range searching behaviour of the livestock.

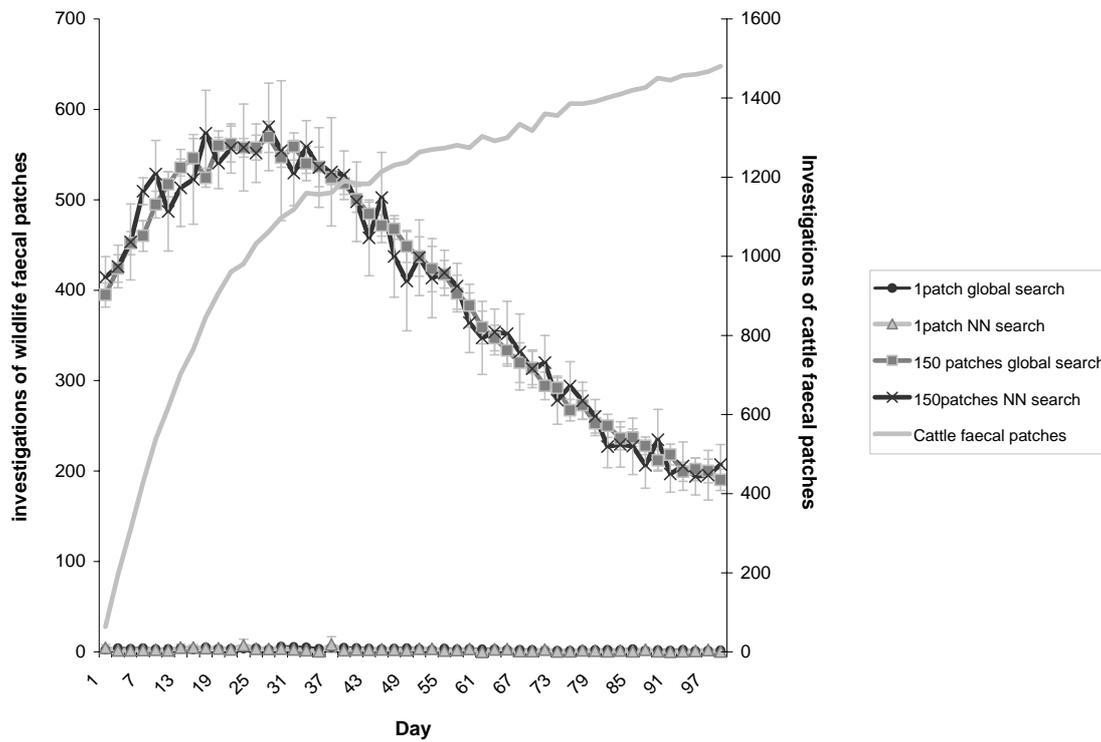


Figure 2: Effect of wildlife faecal defecation pattern and search distance on the number of investigations taken by cattle from wildlife faecal contaminated patches. 1 wildlife faecal contaminated patch is representative of latrine type defecation pattern, and 150 wildlife faecal contaminated patches 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 Figure 1. Figures are the mean number of bites/number of investigations per day averaged over 10 simulations, +/- standard deviation. The daily average number of investigations 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.

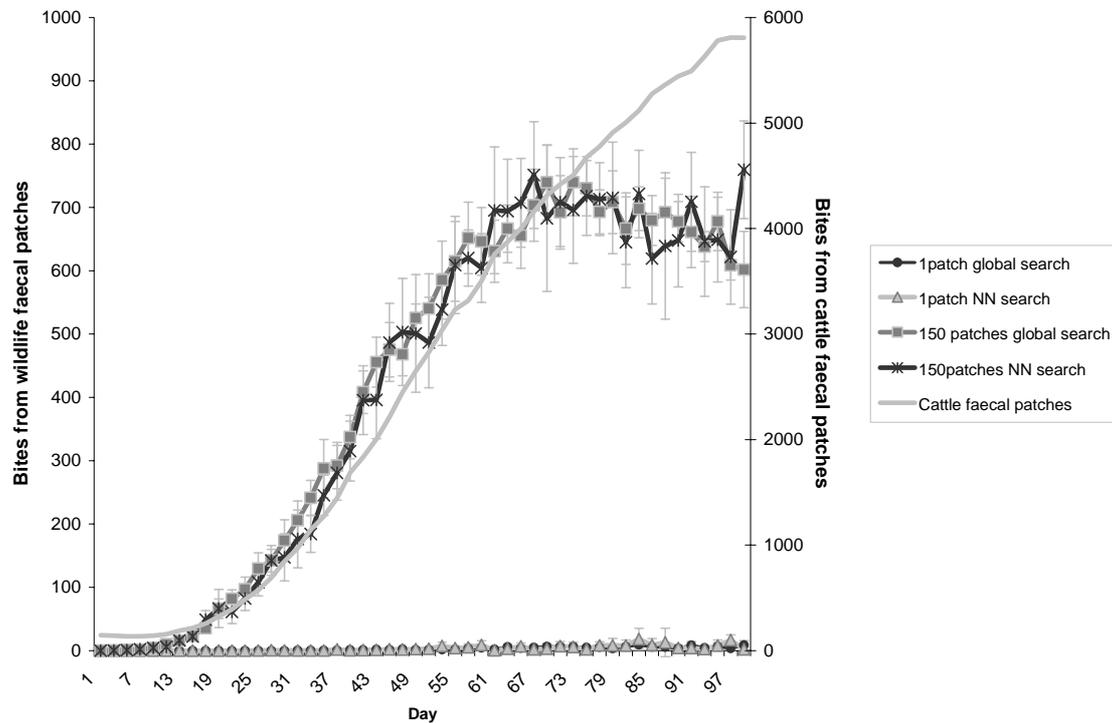


Figure 3: Effect of wildlife faecal defecation pattern and search distance on the number of bites taken by cattle from wildlife faecal contaminated patches. 1 wildlife faecal contaminated patch is representative of latrine type defecation pattern, and 150 wildlife faecal contaminated patches is representative 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 Figure 1. Figures are the mean number of bites/number of investigations per day averaged over 10 simulations, +/- standard deviation. The daily average number of bites taken from patches contaminated with livestock faeces is also shown (see right-hand scale). The results indicate relative insensitivity to searching ability, but that ingestion of faeces is strongly determined by its distribution.

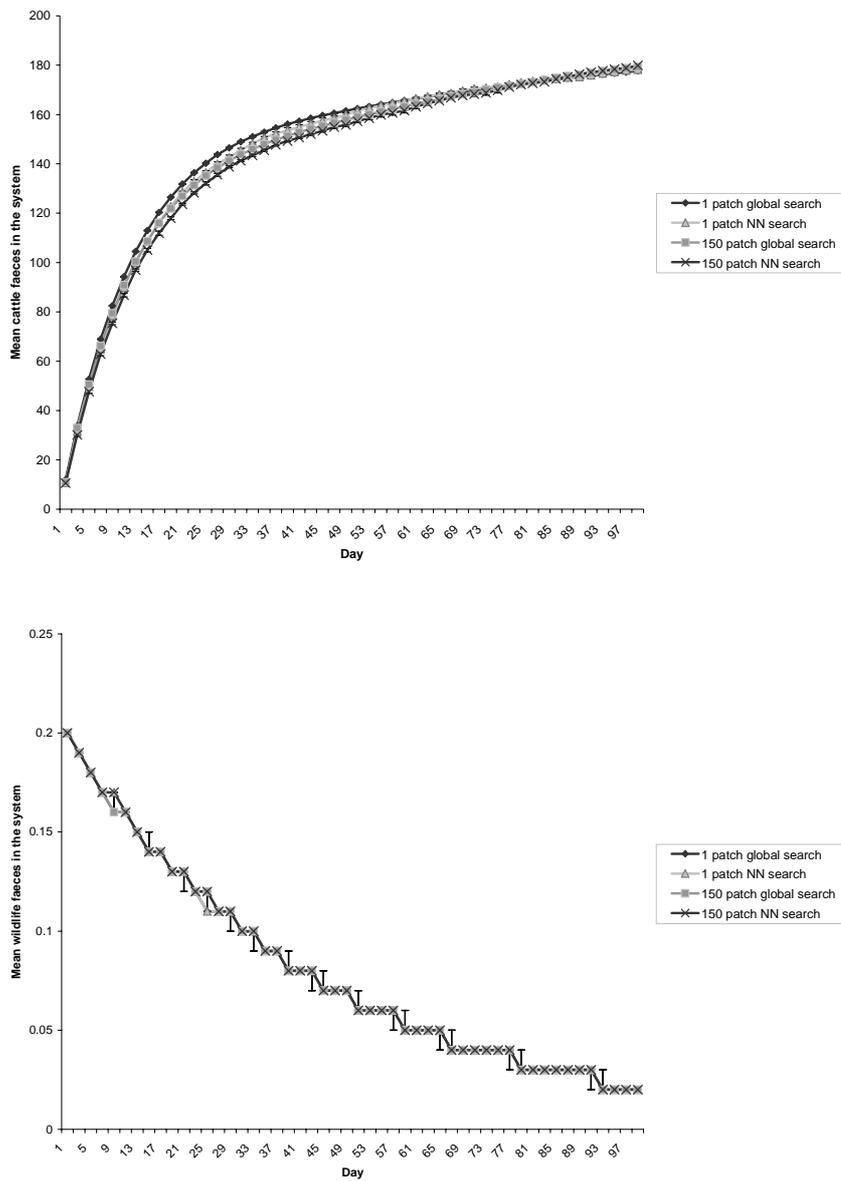
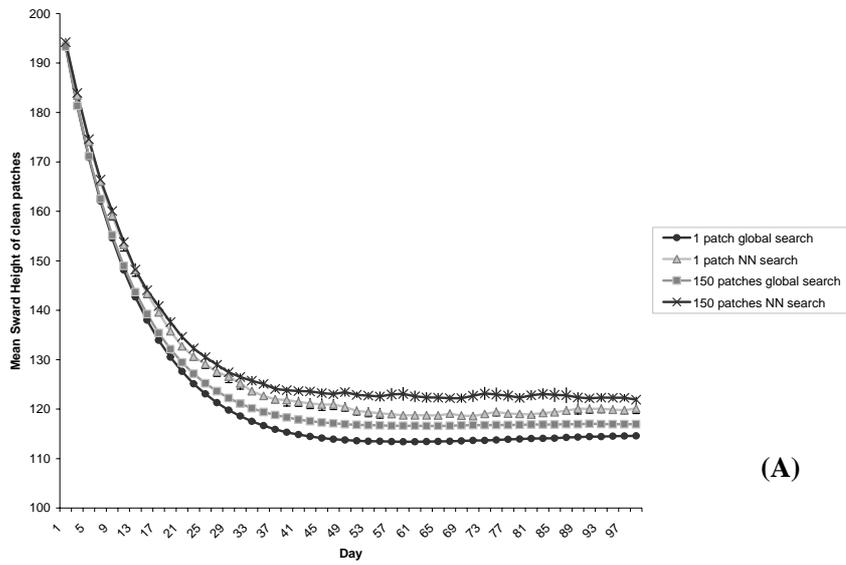
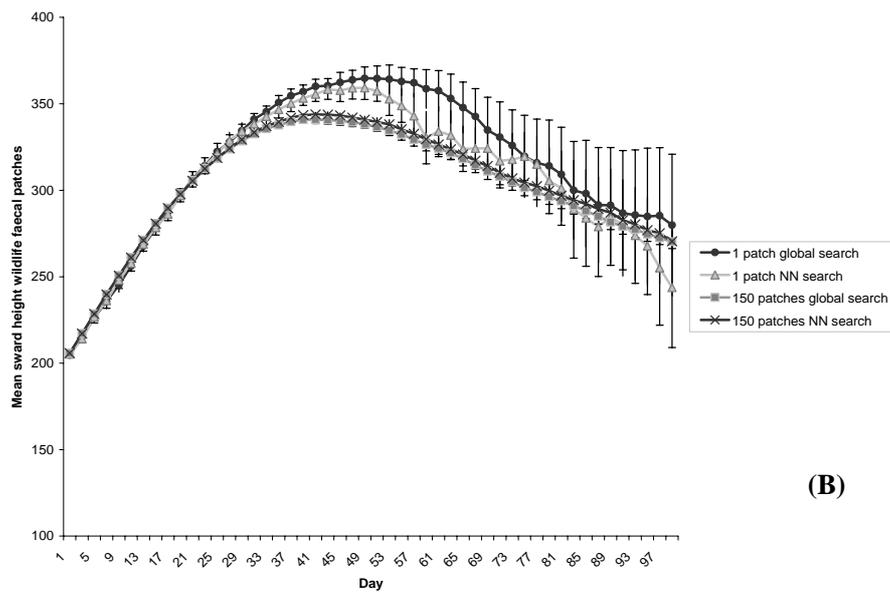


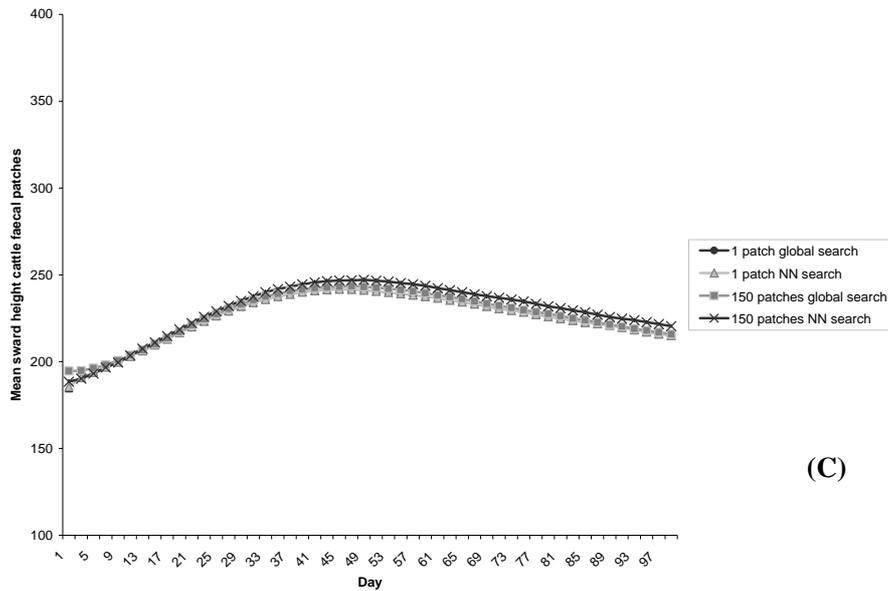
Figure 4: Average faecal contamination levels for livestock (upper graph) and wildlife (lower graph) contaminated patches. Parameter values as in Figure 1. The four sets of results shown relate to different distributions of wildlife faecal contamination (dispersed and clustered) and long and short range 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.



(A)



(B)



(C)

Figure 5: Mean sward height in clean patches (A) and those contaminated with wildlife (B) and livestock (C) faeces. Parameter values as in Figure 1. In each graph the four sets of results shown 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, whilst 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).

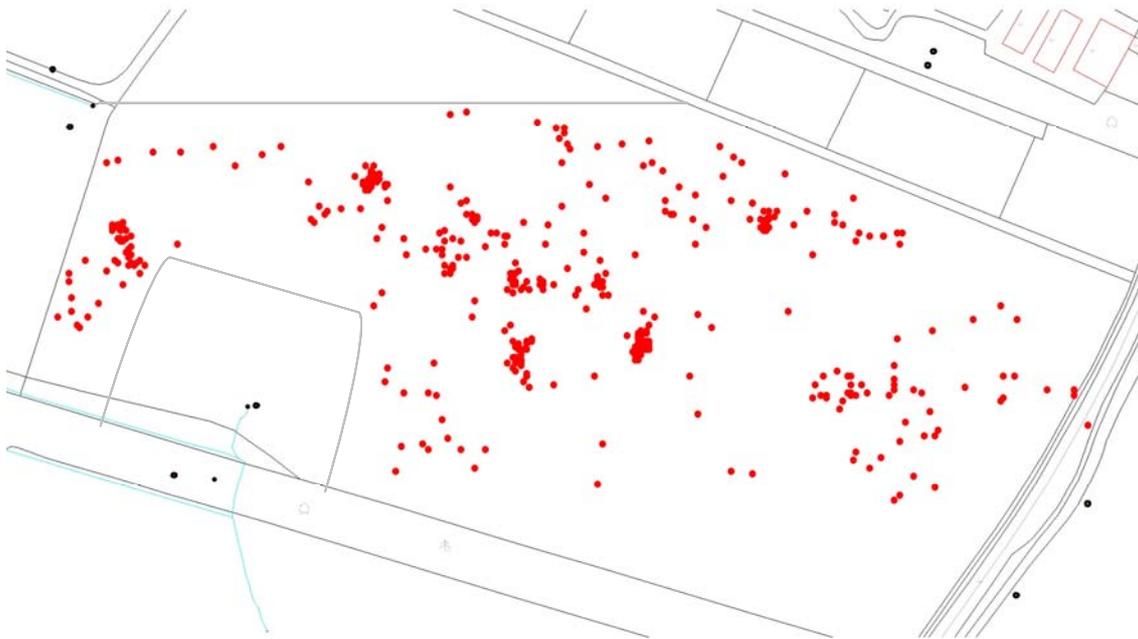


Figure 6. Map of field locations for a single beef cow over a 24 hr period (field size = 6.2 ha, herd size = 40 animals). Global Positioning System location interval was 3 minutes. The 24 hr activity pattern for the animal was chosen at random from an ongoing ITI Scotland Ltd research.