Inter- and intra-specific disease risk: a consequence of behaviour in a complex environment

L. A. Smith[1,4], G. Marion[2], D.L. Swain[3] , P.C.L. White[4] and M.R. Hutchings[1*]

[1]Animal Nutrition and Health, Scottish Agricultural College, West Mains Road, Edinburgh, EH9 3JG, U.K

[2]Biomathematics & Statistics Scotland, JCMB, The King's Buildings, Edinburgh, EH9 3JZ

[3]CSIRO Livestock Industries, JM Rendel Laboratory, Ibis Avenue, North Rockhampton, QLD 4701

[4]Environment Department, University of York, Heslington, York, YO10 5DD

*Author for correspondence (E-mail: Mike.Hutchings@sac.ac.uk)

SUMMARY

Livestock herbivores are at risk of inter- and intra-specific disease transmission via the faecal-oral route during grazing. Each contact between livestock and faeces in the environment is a potential disease transmission event. Cattle behaviour and thus exposure risk varies in relation to the species depositing the faeces and the distribution of the faeces. Here we use a foraging model to simulate the grazing behaviour of beef cattle in two grazing systems (set stock and rotational grazing), to compare the relative inter-specific and intra-specific disease risks via the faecal-oral route under varying scenarios of cattle faecal avoidance behaviour and wildlife defecation patterns. Under both set stock and rotational grazing, defecation pattern has a much stronger effect on disease risk than the level of cattle avoidance, with dispersed defecation patterns representing a significantly greater disease risk in terms of absolute grazing and investigative contact, relative to latrine-type defecation patterns. However, the rate of grazing contacts and investigative contacts with wildlife faecal-contaminated vegetation is greater in rotational grazing systems. Overall, there is a far greater level of intra- versus inter-specific disease risk via the faecal-oral route. However, under certain conditions, particularly for microparasite infections such as paratuberculosis in rabbits and bovine tuberculosis in badgers, wildlife faeces can also pose a significant disease risk. These risks can be enhanced when cattle are first turned out onto pasture and in situations such as low population density or disturbance where intra-specific variations in wildlife behaviour result in more dispersed defecation patterns.

INTRODUCTION

Grazing herbivores must make foraging decisions in grazing environments that are contaminated by host animal faeces. Host animals' faeces may contain both macroparasites (e.g. parasitic helminths) and microparasites (e.g. bacterial pathogens) that can be transmitted via the faecal oral route when grazing [1]. However, herbivores are unable to detect the presence of parasites in the environment, but instead use faeces as a cue for parasites [2]. Thus, herbivores generally avoid grazing near swards contaminated with both their own faeces [3, 4] and faeces of other species [3, 5, 6]. This instinctive behaviour is believed to have evolved as a method of parasite avoidance [7, 8] and has been shown to reduce significantly the grazing herbivore's intake of parasite larvae [9]. However, in both natural systems and agricultural systems, selective grazing to avoid faeces creates a heterogeneous distribution of forage resources consisting of a mosaic of gaps (short, non-contaminated, grazed patches) and tussocks (tall, faeces-contaminated, avoided patches) [10, 11]. Nutrient leaching from faecal deposits results in these faecal-contaminated tussocks of grass having relatively high nutrient contents [12]. Thus the mosaic represents a nutrition versus parasitism trade-off in that the faeces-contaminated tussocks are localized concentrations of both nutritional resources and parasites [13, 14]. Grazing herbivores must make decisions in relation to this trade-off in order to try and maximize the nutritional benefits and minimize the parasitic cost.

Grazing herbivores share their environment with a number of other host animal species, and will come into contact with their own faeces and faeces of other species. Thus, there is the potential for indirect inter-specific and intra-specific disease transmission via the faecal-oral route during grazing. The faeces of different species pose a risk of a variety of different diseases to the grazing herbivore e.g. cattle are at risk of bovine tuberculosis from badger faeces [14] and paratuberculosis from rabbit faeces [15, 16]. Defecation pattern also varies both between species and within species, from single deposits dispersed throughout the environment, to the accumulation of faeces at latrines. For example, rabbits deposit pellets both randomly within their home range and at latrine sites [17]. Badgers tend to accumulate defecations at latrines, although at low densities there are an increasing number of single defecations throughout their habitat [18]. Faeces are often present at latrines for extended periods of time due to wildlife hosts adding fresh faecal contamination. In contrast, for highly dispersed defecation patterns, the faeces will decay from the contaminated patches at a faster rate. For species acting as hosts of disease which is excreted in faeces, these faecal patterns represent patterns of pathogen distribution. Each contact of a susceptible host with faeces (e.g. a bite) represents a potential disease transmission event. Smith (unpublished observations) showed in two separate grazing experiments that cattle vary their grazing response to faeces from different species and to different faecal patterns in the environment. Thus, in isolation these two factors affect the contact rate between herbivores and faeces/pathogens in the environment. However, in a more realistic grazing environment it is the interaction of these two effects that will determine livestock contact with faeces in the environment and therefore the risk associated with different diseases.

Herbivore grazing behaviour in relation to faeces is also affected by the grazing environment (e.g. nutritional environment) [19], therefore grazing management practices which alter the environment will also affect herbivore contact with faeces. Rotational grazing, a practice to optimize pasture growth and productivity, involves the rotation of livestock around a number of paddocks giving each paddock a period of rest for regrowth. This grazing practice allows the herbivore to graze almost all the available pasture in order to stimulate sward growth during the rest period. The grazing pressure in rotational systems is therefore relatively high compared to set stocking where animals continually graze a set pasture size so that grass growth is approximately equal to animal intake. Grazing systems in which the forage availability may become limiting can result in animals being forced to graze faecal-contaminated vegetation and studies have suggested that livestock in rotational systems have increased parasite loads compared with set stocking [20, 21]. Furthermore, farm management practices which intensify the grazing pressure are known to increase livestock contact with badger faeces [6, 22].

The risk of disease transmission to livestock is therefore driven by the interplay between herbivore grazing behaviour, pattern of contamination in the environment and farm management systems. Here we use a spatially explicit individual-based stochastic model that allows simulation of beef cattle grazing behaviour in terms of a trade-off between local visual cues and olfactory cues [23] to determine the impact of these interactions on herbivore contacts with faeces/pathogens in the environment. The first aim of this paper is to simulate the behavioural patterns exhibited by cattle in field experiments (Smith, unpublished observations). The subsequent aims are to use the simulation model to quantify the impact on cattle contact with faeces in the environment of: (1) different levels of cattle avoidance of faeces; (2) different faecal defecation patterns of wildlife; and (3) the interaction of these factors in both set stocking and rotation grazing.

MATERIALS AND METHODS

Model

We use simulation code implementing an extended version of a grazing model [23] (that explicitly captures herbivore contact with faecal contamination in grazing systems (i.e. risk of disease transmission via the faecal-oral rote), to address our objectives. In brief, a series of empirically observed behavioural rules of thumb are used to capture herbivore grazing behaviour in heterogeneous landscapes: 1) herbivores visually asses local neighbourhood to select tall and/or more nutrient rich swards over short and/or nutrient poor swards [24], and 2) herbivores select non-contaminated swards over faecal contaminated swards [6]. However, herbivores have incomplete knowledge of the local environment. Thus the model describes the grazing system as a grid of spatially configured patches, and the selection behaviour of grazing herbivores is captured using a two stage process of herbivore grazing in a heterogeneous environment (Fig.1). Herbivores first select and approach patches based on local visual cues, e.g. sward height and sward nutritional value. The second stage of the selection process is based on local olfactory cues, e.g. faecal contamination at the patch site. Herbivore grazing decisions (selection or rejection of a patch) are determined by the relative strength of these cues. The formulation of the model is described below.

The ordinary differential equation below

$$\frac{dg}{dt} = \gamma g\left(1 - \frac{g}{g_{\max}}\right) - \beta c\left(g - g_0\right), \qquad (1)$$

is a simple, deterministic and non-spatial description of changes in resource density within a grazing system (Note that equation (1) includes no avoidance behaviour.). Here, g is the average sward height, γ is the intrinsic growth rate of the forage resource, $g_{\max}$ the maximum sward height attainable, c the average density of foraging animals and β is the per-capita feeding rate and g_0 represents the ungrazable portion of the sward. In practice, grazing systems are both spatially explicit and subject to stochasticity. The feeding rate is therefore determined by the spatial structure of the sward and the interaction between search rate, search distance and bite rate [25]. Within a non-spatial deterministic model such as (1), mediation and maintenance of the grazing system can be achieved through changes in stocking density and or forage growth rate [26].

Here we formulate an analogous spatially explicit and stochastic model on a unit lattice (i.e. unit spacing between points) of N patches (indexed by $i=1,\ldots,N$) by extending the state-space to represent the sward height g_i and the number of animals c_i at patch i. The total number of animals is N_a. The probability of an animal grazing in its current patch (denoted i), during a small time interval $(t, t+\delta t)$ is

$$\mathrm{P}\big(g_i(t+\delta t) = g_i(t) - 1\big) = \beta c_i(t)\big(g_i(t) - g_0\big)\delta t\ , \qquad (2)$$

where as before g_0 represents the ungrazable portion of the sward. In practice there are instances where animals will overgraze the sward and create bare patches; however within the simulations carried out in this paper the objective was to explore how search rate and search distance mediate spatial heterogeneity. Sward growth is therefore modelled to avoid a climatically induced non-equilibrium phase as would normally be associated with drought conditions and ultimately result in over grazing [27]. Sward growth is formulated as self-limited logistic growth, where the probability of sward growth in patch i during a small time interval $(t, t+\delta t)$ was

$$\mathrm{P}\ \big(g_i(t+\delta t) = (g_i(t) + 1)\big) = \gamma g_i(t)(1 - g_i / g_{\max})\delta t\ , \qquad (3)$$

where γ and $g_{\max}$ are respectively the intrinsic growth rate and maximum sward height. Searching was simulated within a local neighbourhood enabling spatially constrained behavioural selection of grazing resources. Searching was described by the probability of an animal moving from patch i to patch j in a small time interval $(t, t+\delta t)$ as

$$\mathrm{P}\begin{pmatrix} c_i(t+\delta t) = c_i(t) - 1 \\ c_j(t+\delta t) = c_j(t) + 1 \end{pmatrix} = \frac{v}{z(i)} F(i,j)\ c_i(t) g_i(t) \delta t \qquad \forall j \in N_i\ , \qquad (4)$$

where ν is the search rate the normalization factor *z(i) was given by*

$$z(i) = \sum_{j=1}^{N} F\,(i,j) \qquad (5)$$

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

$$F(i,j) = |i-j|^{-s} \qquad (6)$$

The normalization factor *z(i)* ensures that for large *s* (for example >10) animals only search nearest neighbouring patches and the model reduces to the original formulation [23] whilst for $s=0$ the animals search uniformly over the entire arena and the model is closer to the spirit of ref [26]. The characteristic search distance

$$d(s) = \exp\left(\ln(2)/\,s\right) \qquad (7)$$

provides a useful description of this power-law search which measures the distance at which the search rate is half that associated with the nearest neighbours (i.e. on the unit lattice patches for which | i-j | =1) as a fraction of the distance to the nearest neighbours. Therefore as the power law *s* increases, the characteristic search-distance decreases. Note that each of the probabilities (2)-(4) is of the form $R(n \rightarrow n+\delta n)\delta t$ where the state space is denoted by the vector *n* (i.e. a vector containing sward heights g_i and animal numbers c_i for all patches $i=1,\ldots N$) and the event causing a change $n \rightarrow n+\delta n$ occurs at rate

$R(n\rightarrow n+\delta n)$. A summary of all the events included in the model, the rates at which they occur, and the associated change in the state-space is as follows:

$$\begin{array}{rcccr} R(n\rightarrow n+\delta n) & \delta g_i & \delta c_i & \delta c_j & \\ \gamma g_i(1-g_i/g_{\max}) & +1 & 0 & 0 & \text{Growth at } i \\ \beta c_i(g_i-g_0) & -1 & 0 & 0 & \text{Bite at } i \\ \dfrac{\nu}{z(i)}F(i,j)\;c_i\;g_j & 0 & -1 & +1 & \text{Move } i\rightarrow j \end{array} \qquad (8)$$

The model above is fully described in ref [28] which builds on ref [23], and has been further extended here as follows. The treatment of herbivore faeces has been extended to describe the production of faeces from the grazing herbivore (Equation 9), the decay of herbivore faeces (Equation 10) and the grazing herbivore's avoidance of its own species' faeces (Equation 11). The production of faeces is modelled by augmenting the state-space with with a variable s_k representing the stomach contents the stomach contents of animal $k = 1,\ldots,N_a$. When animal k grazes the stomach contents are increased by 1. Animal k defacates at rate

$$f_{dep}(s_k - s_0) \quad \text{for } s_k > s_0 \text{ (zero otherwise),} \qquad (9)$$

and if it is currently located at patch i defacation increases the local faecal contamination f_i by s_0.

The faecal deposit decays exponentially at rate f_{dk}. Thus $f_i \rightarrow f_i - 1$ at rate

$$f_i\,f_{dk} \qquad (10)$$

If the faeces level at patch $i = 1,\ldots\ldots,N$ is f_i then avoidance is modelled simply by reducing the bite rate for each animal at patch *i* by a factor $e^{-\mu f_i}$. Thus the total bite rate across all animals at patch *i* becomes

$$\beta c_i(t)(g_i(t) - g_0)\ e^{-\mu f_i} \qquad (11)$$

Wildlife faeces are treated as exponentially decaying reservoirs, which are avoided in the same manner, but to a potentially different extent, as herbivore faeces (Equation 12). In order to explore the effect of avoidance of other faeces, two additional faecal contaminations have been added to the model. At patch *i* these contaminations are described by the amount of other faeces from two species, a and b, as fa_i and fb_i respectively. The deposition of other faeces is not modelled, and from an initial level of contamination (which must be defined), the amount of faeces present is assumed to decay exponentially as before (see equation 10), but with decay rates fa_{dk} and fb_{dk}. Avoidance of other faeces is also modelled analogously to the treatment of the herbivore's faeces, but with different levels of avoidance μ_a and μ_b. Thus the combined effect of all faecal contamination modified the total bite rate across all animals at patch *i* to

$$\beta c_i(t)(g_i(t) - g_0)\exp(-[\mu f_i + \mu_a\ fa_i\ + \mu_b\ fb_i\ ]) \qquad (12)$$

An additional feature which was added to the model is the concept of an individual animal's daily intake requirement, denoted R_k for animal *k*. Within a given day, animal *k* will continue grazing until the intake accumulated over the current day reaches R_k, at which point it stops grazing until the following day when this process is repeated.

To describe a range of different management practices, such as set stocking and rotation, the model allows the animals to be repeatedly removed and returned to the pasture. During the periods when the animals are absent from the system, sward growth and faecal decay continue as before, but grazing and defecation are suspended. When the animals return to the pasture, their accumulated intakes are reset to zero.

Parameterisation

The model was parameterized to simulate a grazing situation with three beef cows in a set-stocking scenario, except for the rotational grazing scenario specified below. It was important to ensure the simulations replicated the spatial scale of agricultural systems as disease transmission occurs on a bite by bite basis. Thus, all simulations were carried out in a 70 x 70 patch lattice, where each patch represented 0.5m^2, the approximate area of one cattle faecal pat and the rejected area around it [29]. The lattice represented a pasture of 0.25ha. The simulation size was a compromise between the duration of individual runs of the model and the number of animals in the system. The set stocking parameters i.e. where mean grass height is stable and sward growth is equal to herbivore intake (sward growth rate γ=0.00004; initial sward height g_{start}=200; maximum sward height g_{max}=400) were calculated from a herbivore grazing rate (β) that represented approximately 30000 bites of herbage a day (β = 0.1) [29], and a search rate (nu) that represent a cattle step rate of approximately 3 steps a min [30] (nu = 0.015). The search distance of herbivores is currently unknown. However, due to the high movement rate of cattle in the relatively small field sizes used in agricultural systems, cattle contact rates with faeces are insensitive to search distance [31]. As a result, the search distance coefficient was set to nearest neighbour (s=10), where the grazing herbivore only searches nearest neighbour patches for all the simulations described. At the start of the simulation, cattle were introduced into a pasture free of any cattle faecal contamination ($f_i = 0 \quad \forall i=1,\ldots,N$) and cattle deposited faeces approximately 10-15x a day [29] (f_{dep} = 1.0, s0=2000.0). Each individual animal's daily intake requirement was not set, allowing the animals to graze the whole day. Cattle faeces had a decay rate, where degradation to approximately 10% of the initial faecal deposit would occur 3 months after deposition [12] (f_{dk} = 0.00001776). Initial response by cattle to their own fresh faeces was set at almost complete avoidance [3] (μ=0.0025, corresponding to a bite rate from freshly faecal-contaminate patches of less than one percent of the bite rate from clean patches). In order to allow a contrast between levels of inter- and intra-specific contact with faeces, additional faeces were added to the system and were parameterized to represent different scenarios of wildlife faeces as described in the model runs performed. All the simulations were run for 100 days, which, for the set stock scenarios, allowed intake and sward heights to reach equilibrium.

Model runs performed

Cattle avoidance of wildlife faeces. To investigate the impact of varying the level of cattle avoidance of wildlife faeces in isolation, simulations were run with six levels of cattle avoidance for each patch of wildlife faeces. A herbivore's avoidance level of a patch is dependent on the amount of faeces within it. Thus, in all simulations for cattle avoidance of wildlife faeces, there were 150 randomly selected patches contaminated with faeces. Each contaminated patch had 6.67 units of wildlife faeces, giving the same defecation pattern and the same total amount of wildlife faeces in the environment (1000 units). The avoidance levels simulated were μ_a=0 (cattle initially show no avoidance of fresh wildlife faeces, representative of cattle avoidance of rabbit faeces [15]), μ_a=0.15, μ_a=0.3, μa=0.45, μ_a=0.6, μ_a=0.75 (cattle initially show almost complete avoidance of fresh wildlife faeces, representative of badger faeces [6]). In order to consider cattle avoidance of wildlife faeces in isolation, all wildlife faeces in the environment were set to have no decay (fa_{dk} =0).

Defecation pattern. To investigate defecation pattern in isolation, simulations were run with four different defecation patterns with the same total amount of wildlife faeces in the environment (1000 units), varying the number of contaminated patches. The numbers of contaminated patches simulated were 1 patch (representative of a latrine type defecation pattern), 50 patches, 100 patches and 150 patches (representative of single dispersed deposit defecation patterns). In all cases the contaminated patches were selected at random. The initial level of avoidance by cattle of each patch contaminated with wildlife faeces was set to represent 'almost complete' avoidance, i.e. the same degree of avoidance that cattle show towards their own faeces. As a herbivore's avoidance level of a patch is dependent on the amount of faeces in the contaminated patch, in order to get the same initial level of avoidance, μ_a varied for each defecation pattern (1 patch, μ_a = 0.005; 50 patches, μ_a = 0.25; 100 patches, μ_a = 0.5; 150 patches, μ_a = 0.75). To investigate the effect of defecation pattern in isolation, all wildlife faeces in the environment were set to have no decay (fa_{dk} = 0).

Interaction between level of avoidance behaviour and wildlife defecation pattern

(a) Set stock grazing

To investigate the interaction between avoidance level and wildlife defecation pattern within a set stocking context, four scenarios were modelled with two defecation patterns (the same total amount of wildlife faeces in the environment (1000 units), varying the number of contaminated patches) and two levels of cattle avoidance: (1) a single contaminated patch (representing a latrine-type defecation pattern), with no cattle avoidance of wildlife faeces (μ_a=0); (2) a single contaminated patch (latrine type defecation pattern) and almost complete avoidance (for 1 patch contaminated μ_a=0.005); (3) 150 contaminated patches (representing a dispersed defecation pattern) and no cattle avoidance of wildlife faeces (μ_a=0); (4) 150 contaminated patches (representing a dispersed defecation pattern) and almost complete avoidance of wildlife faeces (for 150 contaminated patches μ_a=0.75). In order to include the effect of faecal decay, wildlife faecal decay rate was set so that at the end of the simulation (day 100), 10% of the initial wildlife faeces remained in the system (fa_{dk} =0.00001599).

Rotation grazing, The same four scenarios described in the previous section were also used to investigate the interaction effects of defecation pattern and cattle level of avoidance of wildlife faeces within a rotational grazing scenario. For rotational grazing, the set stock pasture was divided into two pastures and three cattle were rotated round each pasture twice. Only one of the pastures was simulated, thus the simulations were carried out on a 49 x 50 patch lattice. Each patch represented 0.5m^2 and the whole lattice represented a pasture of 0.125ha, half the size of the set stock pasture. The rotation was 25 days in the simulated pasture, 25 days out, so that two complete rotations lasted 100 days. To prevent ‘unrealistic’ overgrazing on the first day back in the pasture, the cattle’s daily intake requirement was set to the equivalent daily intake of cattle in a set stock environment (dR_k = 9000).

Measurements of forage availability

For the realistic grazing scenarios, i.e. the set stock and rotation grazing, measurements of grass availability were gathered to ensure the model successfully created a heterogeneous gap and tussock mosaic, and thus presented the grazing cattle with the nutrition versus parasitism trade-off. The following statistics for grass availability were gathered over the 10 repeated stochastic simulations:

1. The mean forage availability (number of bites available per 0.5m^2) of wildlife faecal-contaminated patches with high cattle avoidance. No measurements of forage availability were gathered for wildlife faecal-contaminated patches with no cattle avoidance as tussocks would not form at these patches due to the non-avoidance of the faeces.
2. The mean forage availability (number of bites available per 0.5m^2) of cattle faecal-contaminated patches
3. The mean forage availability (number of bites available per 0.5m^2) of non-faecal-contaminated patches.

Measurements of cattle grazing behaviour

The grazing statistics (model outputs) were gathered over 10 repeated stochastic simulations for each scenario described above.

1. No. of bites from wildlife faecal-contaminated patches per day
2. No. of investigations of wildlife faecal-contaminated patches per day. An investigation was defined as a visit to a patch with no bites.
3. No. of bites from cattle faecal-contaminated patches per day.
4. No. of investigations from cattle faecal-contaminated patches per day.

RESULTS

Forage availability in the set stock and rotation grazing systems. Overall the mean number of bites of forage available in a $0.5m^2$ patch of wildlife faecal-contaminated patches and cattle faecal-contaminated patches was greater than the mean number of bites of forage available in a $0.5m^2$ patch of clean non-contaminated patches in both set stock and rotational grazing systems (Fig. 2). In the set stock system, at the maximum difference in forage availability, wildlife faecal-contaminated patches and cattle faecal-contaminated patches had 2.6 times and 2 times greater forage availability than the non-contaminated patches, respectively (Fig 2A). Similarly, in the rotational grazing system, at the maximum difference in forage availability, wildlife faecal-contaminated patches and cattle faecal-contaminated patches had 3 times and 2.3 times greater forage availability than the non-contaminated patches, respectively (Fig. 2B).

Cattle avoidance of wildlife faeces. Increasing cattle avoidance of wildlife faeces is associated with a decrease in the number of cattle bites from wildlife faecal-contaminated patches both pre- (days1-30) and post-system equilibrium (days 31-100). However, post-equilibrium there is no difference in grazing contact levels between the three lowest avoidance levels (μ_a = 0, 0.15 and 0.3) (Fig. 3A). Increasing cattle avoidance of wildlife faeces is associated with an increase in the number of investigations of wildlife faecal-contaminated patches both pre- and post-equilibrium (Fig. 3B). The overall number of bites and number of investigations from cattle faecal-contaminated patches is significantly greater than the number of bites/investigations from wildlife faecal-contaminated patches (i.e. up to 46 times more bites and up to 14 times more investigations) (Figs. 3A & 3B).

Defecation pattern. Increasing the number of faecal-contaminated patches (i.e. more dispersed faecal-contamination patterns) is associated with an increasing number of cattle bites and investigations from wildlife-contaminated patches both pre- (days1-50) and post-equilibrium (days 41-100) (Figs. 4A & 4B). However, the relative numbers of both grazing contacts and investigative contacts are less than commensurate with area. For example, defecation patterns with 150 contaminated patches lead to approximately only 90 times greater number of bites compared to single patches. Additionally, defecation patterns with 150 contaminated patches lead to approximately 100 times greater number of investigations of wildlife-contaminated patches. The overall number of bites and number of investigations from cattle-contaminated patches is significantly greater than the number of bites/investigations from wildlife faecal-contaminated patches (i.e. up to 4251 times more bites and up to 191 times more investigations) (Figs. 4A & 4B).

Set stock grazing. The combined effects of avoidance and defecation pattern are consistent with the effects in isolation as modelled in previous simulations (Figs. 5A & 5B). Thus, increased cattle avoidance of wildlife faeces results in reduced grazing contacts and increased investigative contact with wildlife faecal-contaminated vegetation. Defecation patterns with a greater number of contaminated patches result in increases in both grazing and investigative contacts. When comparing the magnitude of effects, level of faecal avoidance has a lesser effect than defecation pattern on the number of cattle contacts with faeces, e.g. dispersed patterns of both avoidance levels have a significantly greater number of grazing contacts and investigative contacts relative to single latrine patches (Figs. 5A & 5B). However, this observed increase in contacts with the number of contaminated patches is not commensurate with the area contaminated, e.g. 150 contaminated patches result in only 105 times more bites than 1 contaminated patch. (Table.1). Pre–equilibrium (days 1-39), grazing contacts with wildlife faeces are greatest in scenario 3 (dispersed wildlife faeces and no cattle avoidance). In contrast, grazing contacts are greatest post-equilibrium (days 40-100) in scenario 4 (dispersed wildlife faeces and high cattle avoidance; Fig. 5A). Investigative contacts with wildlife faeces are highest in scenario 4 throughout the simulation (Fig. 5B). The overall number of bites and number of investigations from cattle faecal-contaminated patches are significantly greater than the number of bites/investigations from wildlife faecal-contaminated patches (up to 379 times more bites and up to 1463 times more investigations; Figs. 5A & 5B).

Rotation grazing. Under rotation grazing, the effects of cattle avoidance of faeces and defecation pattern, both singly and in combination, are consistent with the patterns observed in a set stock environment (figs 6A & 6B). However, the non-commensurate increase in both grazing contact and investigative contact associated with dispersed defecation patterns (150 contaminated patches) under set stock conditions does not occur. In the rotational grazing scenario, the increase in grazing and investigative contact is commensurate with the area/number of patches contaminated (Table 1). A comparison of the interaction effects of avoidance and wildlife defecation pattern in a set stocking and a rotational grazing scenario (Figs 6A & 6B) shows that, per unit time spent in the pasture, there are a greater number of grazing contacts and investigative contacts with wildlife faecal-contaminated vegetation in rotational grazing systems. In the rotation grazing, the number of investigative contacts are highest in scenario 4 (dispersed wildlife faeces and high cattle avoidance) during both the first (days 1-25) and second rotation (days 51-75) (Fig. 6B). In contrast, grazing contacts are not consistent across the first and second rotations. During the first rotation, grazing contacts are greatest in scenario 3 (dispersed wildlife faeces and no cattle avoidance). During the second rotation, the number of grazing contacts is highest in scenario 4 (Fig. 6A). The overall number of bites and number of investigations (i.e. total contact) from cattle faecal-contaminated patches are significantly greater than the number of bites/investigations from wildlife faecal-contaminated patches (i.e. up to 163 times more bites and up to 1198 times more investigations) (Figs. 6A & 6B). However, during the first rotation, there are a greater number of bites from wildlife faeces both in a dispersed defecation pattern with no cattle avoidance, and a dispersed defecation pattern with high cattle avoidance. There is also a greater number of investigations of wildlife faeces in a dispersed wildlife defecation pattern with high cattle avoidance relative to the number of bites and investigations from patches contaminated with cattle faeces (Figs 6A & 6B).

DISCUSSION

The aim of this study was to determine the interactions between herbivore behaviour and the environment during grazing and their subsequent impact on the contact process between grazing herbivores and faeces/pathogens in the environment. These contact patterns can then be applied to quantifying the relative risk of specific diseases transmitted to livestock via the faecal-oral route. The first step in this study was to determine if the model successfully simulated the heterogeneous sward structure representing the nutrition versus parasitism trade-off. In both the set stock and rotational grazing scenarios, the faecal-contaminated patches (both wildlife and cattle) had significantly greater mean grass heights relative to the non-contaminated patches. Thus a heterogeneous sward structure had been created in all the grazing systems, suggesting that the behavioural rules of thumb governing herbivore grazing in the model were adequate for representing real environments i.e. the emergent properties of the model match empirical observation. Furthermore, the costs and benefits of this dynamic system were also similar to actual systems in that faecal-contaminated patches provide localized concentrations of both nutritional resources and parasites.

To allow for a comparison between livestock behavioural patterns simulated by the model and those observed in cattle grazing experiments (Smith et al, unpublished), the individual effects of cattle avoidance of faeces and faecal defecation pattern were simulated in a simple system with no faecal decay. In order to simulate cattle avoidance of different types (species) of faeces the model was parameterized to simulate a range of different avoidance levels from no initial avoidance (representative of rabbit faeces) to almost complete initial avoidance (representative of badger faeces). Here this step-wise increase in the level of cattle avoidance resulted in fewer grazing contacts with faecal-contaminated patches for each level of avoidance, when cattle are first placed in the pasture. Once cattle are in agricultural systems, their grazing behaviour is also influenced by the availability of grass in the system. Due to the initial avoidance of faecal-contaminated areas and further contamination of clean pasture, the decreasing amount of clean grass available may force cattle to graze faecal-contaminated areas [32]. This has been effectively simulated in the model, with a gradual increase in the number of bites with time from faecal-contaminated patches for all avoidance levels. In contrast, the reduction in bites with time from faecal-contaminated patches under conditions of no faecal avoidance is driven by the reduction of grass availability at the faecal-contaminated patches. Thus, the model successfully produced the range of cattle faecal avoidance behaviours as expected. Therefore, cattle avoidance of the faeces of different wildlife hosts can be placed in the context of the model. For example, cattle show strong initial avoidance of both badger faeces and their own faeces; and no avoidance of rabbit faeces (Smith et al, unpublished). This will have implications for the contact rates of cattle with the different infectious agents excreted in faeces by these different species.

The varying defecation pattern scenarios demonstrated that dispersed defecation patterns result in a greater amount of grazing contacts and investigative contacts than latrines. The grazing contact simulated here is consistent with the grazing study by Smith et al (unpublished), in which cattle grazed badger faecal-contaminated patches in a more dispersed faecal pattern faster than those concentrated in a single patch (i.e. representative of latrines). Thus the model has simulated successfully the patterns of grazing contact by cattle shown towards different types of faeces and different faecal defecation patterns.

In the more realistic set stock grazing scenarios (the interaction of avoidance and defecation pattern with faecal decay), the effects of avoidance and defecation pattern are similar to the effects of these factors in isolation. However, defecation pattern has a much stronger effect on disease risk than the level of cattle avoidance, with dispersed defecation patterns representing a significantly greater disease risk in terms of absolute grazing and investigative contact, relative to latrine-type defecation patterns. The risk of disease via grazing contact is also affected by the phase of the grazing process. In the early phase of set stocked grazing (pre-equilibrium), cattle have the greatest grazing contact with wildlife faeces where these faeces are dispersed and there is no cattle avoidance of them. The scenario of dispersed wildlife faeces and no cattle avoidance is representative of rabbit faeces and badger urinations, as cattle show no avoidance of either [6, 16] and they can both occur dispersed throughout the pasture [17, 34]. Microparasite numbers (e.g. *Mycobacterium*) are at their maximum and pose the greatest disease risk when faeces are first deposited in the environment [33]. Rabbit faeces pose a risk of paratuberculosis (*Mycobacterium avium* subsp *paratuberculosis*) containing up to 4×10^6 colony forming units/g faeces [35]. Badger urinations pose a major risk of bovine tuberculosis (*Mycobacterium bovis*) containing up to 3×10^5 colony forming units per ml of urine [36]. There will therefore be an enhanced risk of transmission of these diseases via the faecal-oral routes when cattle are first placed on a pasture.

The patterns of contact observed in set stock grazing are similar to those in the rotational grazing scenario. Thus, during the first rotation of the rotation grazing scenarios, when cattle are first placed in the pasture, cattle have the greatest number of grazing contacts when wildlife faeces are dispersed and there is no cattle avoidance (i.e. representative of rabbit faeces and badger urinations). However, under rotation grazing, this risk is also amplified relative to the risk in a set stock environment. The greater levels of contacts in rotation grazing are largely driven by the increased stocking density in this grazing system. Whilst grazing, livestock selectively graze non-contaminated pasture and further contaminate clean areas with their own faeces. Thus, in rotational grazing the cattle are forced to graze fresh faeces faster and therefore increase their exposure to microparasite diseases such as paratuberculosis and bovine tuberculosis.

In all of the grazing scenarios here, cattle have a greater overall number of grazing contacts and investigative contacts with their own faeces relative to the contacts with the wildlife faeces in the system. The simulations indicate that a major factor that drives cattle contact with faeces in grazing systems is the area of pasture that is contaminated.

In agricultural systems, often a greater proportion of the pasture is covered by cattle faeces compared to the area covered by wildlife faeces, resulting in cattle contacting their own faeces more. Furthermore, for the grazing contacts with cattle faeces, there is an initial strong avoidance in the pre-equilibrium stage of the set stock scenario, and in the first rotation of the rotation grazing scenario. This results in cattle faecal-contaminated patches being relatively tall and attractive to the cattle, which drives the increase in grazing contact with faeces post-equilibrium in the set stock scenario, and in the second rotation of the rotation grazing. Macroparasites take a number of weeks to develop into infective stage larvae and migrate from the faeces into the surrounding sward, where they represent a risk of infection [37], and some wildlife species may harbour macroparasites that can infect cattle, e.g. wild deer have been implicated in the transmission of lungworm (*Dictycaulus* spp) to domestic cattle [38, 39]. However, the patterns of cattle grazing contact between both wildlife faeces and cattle faeces simulated here suggest that any macroparasite infections arising from cattle faeces will pose a more immediate risk than those associated with wildlife faeces..

Contact with a pathogen in the environment and the risk of disease from that pathogen is further complicated by the dose required for an effective transmission event e.g. infection. Dose-response assessment typically predicts that the probability of infection increases with increasing dose of a pathogen, in the shape of a sigmoid curve. In the simulations here, each contaminated patch in the dispersed faecal patterns contains fewer units of faeces, and therefore may have a lower dose of pathogen per patch. In contrast, at latrine sites, it is likely that there will be a far higher dose of pathogens present in the patch. Currently, there are no definitive data to describe the relationship between exposure to pathogens in the environment and infection via the faecal-oral route. However, the disease risk associated with different faecal patterns will be dependent on the dose of the pathogen at a single patch, and the corresponding probability of infection on the dose-response sigmoid curve. If the dose of pathogen present in one dispersed faecal patch falls before the plateau of the sigmoid curve, the corresponding probability of infection for one contact with a dispersed patch will be less than the probability of infection for one contact with a latrine patch, which will have a greater dose of pathogen. In a number of the grazing scenarios simulated here (e.g. the set stock grazing), the overall increase in grazing contact with dispersed faecal patterns relative to the grazing contacts to latrine faecal patterns is a less than commensurate to the area of pasture contaminated. Thus in these situations, latrine-type defecation patterns may pose a greater risk of disease compared to dispersed faecal patterns. In contrast, in the rotation grazing scenarios, the overall increase in grazing contact with dispersed faecal patterns relative to the grazing contact with the latrine faecal patterns is commensurate with the area of pasture contaminated, indicating that absolute contacts may provide a better indication of disease exposure. If the dose from one dispersed faecal patch falls after the plateau of the dose-response sigmoid curve then the corresponding probability of infection for one contact with a dispersed patch will be equal to the probability of infection for one contact with a latrine patch. Thus, the absolute contacts will determine risk of disease and a dispersed defecation pattern will pose a greater risk of disease relative to the latrine faecal patterns. The number of contacts relative to the area contaminated is also affected by the grazing phase. In the pre-equilibrium phase of set stock grazing, there is a greater than commensurate increase in both grazing and investigative contacts for dispersed faecal patterns with high cattle avoidance, relative to the area of pasture contaminated. This is of applied significance for the management and prevention of wildlife disease. For example, when cattle are first placed on a pasture in areas with bovine tuberculosos in badgers, there may be a greater risk of infection from faeces in areas of lower badger density (where faeces may be more dispersed) than in areas of high badger density (where faeces are concentrated at latrine sites). Similarly, the risk of infection may be increased by disturbance of the badger population during culling operations, resulting in a more dispersed pattern of defecation.

In conclusion, the contact patterns between grazing cattle and distributions of faeces/parasites in the environment play an important role in the risk of disease transmission via the faecal-oral route. The results of the simulations, in combination with the often greater amounts of livestock versus wildlife faeces in the agricultural systems, highlight the far greater risk of intra- versus inter-specific disease risk via the faecal-oral route. However, under certain conditions, particularly for microparasite infections, wildlife faeces can also pose a significant disease risk. Our model has quantified how this risk can be modified by different patterns of cattle avoidance behaviour, wildlife faecal deposition in the environment and cattle husbandry practices, with rotation grazing systems posing a greater risk of disease transmission to grazing cattle compared to set stock grazing systems. Further investigations of the relationship between exposure to a specific dose of pathogen in the environment and subsequent infection are required to quantify the risk of infection associated with these behavioural contact patterns for specific disease scenarios.

ACKNOWLEDGEMENTS

The Scottish Agricultural College and Biomathematics & Statistics Scotland receives support from the Scottish Executive Environment and Rural Affairs Department (SEERAD). MRH receives support from a SEERAD senior research fellowship.

DECLARATION OF INTEREST

None

REFERENCES

1. Sykes AR. Endoparasites and herbivore nutrition. In: Hacker JB, Ternouth JH, eds. *The Nutrition of Herbivores*. Harickvale, Australia: Academic Press, 1987, pp. 211-232.
2. Cooper J, Gordon IJ, Pike AW. Strategies for the avoidance of faeces by grazing sheep. *Applied Animal Behaviour Science*. 2000; 69: 15-53.
3. Forbes TDA, Hodgson J. The Reaction of Grazing Sheep and Cattle to the Presence of Dung from the Same or the Other Species. *Grass and Forage Science.* 1985; 40: 177-182.
4. Hutchings MR, *et al*. Behavioural strategies used by parasitized and non-parasitized sheep to avoid ingestion of gastro-intestinal nematodes associated with faeces. *Animal Science*. 1998; 67: 97-106.

5. Benham PF, Broom DM. Responses of dairy cows to badger urine and faeces on pasture with reference to bovine tuberculosis transmission. *British Veterinary Journal*. 1991; 147: 517-532.
6. Hutchings MR, Harris S. Effects of farm management practices on cattle grazing behaviour and the potential for transmission of bovine tuberculosis from badgers to cattle. *Veterinary Journal*. 1997; 153: 149-162.
7. Hart BL. Behavioral Adaptations to Pathogens and Parasites - 5 Strategies. *Neuroscience and Biobehavioral Reviews*. 1990; 14: 273-294.
8. Lozano GA. Optimal Foraging Theory - a Possible Role for Parasites. *Oikos.* 1991; 60: 391-395.
9. Michel, J. F. (1955) Parasitological Significance of Bovine Grazing Behaviour. *Nature*. 1955; 175: 1088-1089.
10. Hutchings MR, Kyriazakis I, Gordon IJ. Herbivore physiological state affects foraging trade-off decisions between nutrient intake and parasite avoidance. *Ecology*. 2001; 82: 1138-1150.
11. Crawley MJ *et al*. Vegetation and sheep population dynamics. In: Clutton-Brock T, Pemberton J, eds. *Soay sheep: dynamics and selection in an island population.* Cambridge; Cambridge University Press, 2004. pp. 89-112.
12. Haynes RJ, Williams PH. Nutrient cycling and Soil Fertility in the Grazed Pasture Ecosystem. *Advances in Agronomy*. 1993; 49: 119-199.
13. Hutchings MR, *et al*. The herbivores' dilemma: trade-offs between nutrition and parasitism in foraging decisions. *Oecologia*. 2000; 124: 242-251.

14. Muirhead RH, Gallaghe J, Burn KJ. Tuberculosis in Wild Badgers in Gloucestershire - Epidemiology. *Veterinary Record*. 1974; 95: 552-555.

15. Daniels MJ, *et al*. The grazing response of cattle to pasture contaminated with rabbit faeces and the implications for the transmission of paratuberculosis. *Veterinary Journal*. 2001; 161: 306-313.

16. Judge J, *et al*. Ingestion of faeces by grazing herbivores - risk of inter-species disease transmission. *Agriculture Ecosystem & Environment*. 2005; 107: 267-274.

17. Sneddon IA. Latrine Use by the European Rabbit (Oryctolagus-Cuniculus). *Journal of Mammalogy*. 1991; 72, 769-775.\

18. Hutchings MR, Service KM, Harris S. Defecation and urination patterns of badgers Meles meles at low density in south west England. *Acta Theriologica*. 2001; 46: 87-96.

19. Smith LA, White PCL, Hutchings MR. Effect of the nutritional environment and reproductive investment on herbivore-parasite interactions in grazing environments. *Behavioral Ecology*. 2006; 17: 591-596.

20. Cordia H, *et* al. Effect of rotational grazing systems on gastrointestinal nematodes in beef yearlings. *American Journal of Veterinary Research*. 1964; 25: 1473-1478.

21. Kunkel JR, Murphy WM. Effect of Stocking Rate, Grazing System, and Fenbendazole Treatment on Subclinical Parasitism in Dairy Heifers. *American Journal of Veterinary Research*. 1988; 49: 724-727.

22. Scantlebury M, *et al*. Risk of disease from wildlife reservoirs: Badgers, cattle, and bovine tuberculosis. *Journal of Dairy Science*. 2004; 87: 330-339.

23. Marion G, Swain DL, Hutchings MR. Understanding foraging behaviour in spatially heterogeneous environments. *Journal of Theoretical Biology*. 2005; 232: 127-142.

24. Bazely DR. Rules and cues used by sheep foraging monocultures. In: Hughes H, eds. *Behavioural Mechanism of Food Selection.* London; Springer, 1990. pp 343-367.

25. WallisDeVries MF, Laca EA, Demment MW. From feeding station to patch: scaling up food intake measurements in grazing cattle. *Applied Animal Behaviour Science*. 1998; 60: 301-315.

26. Schwinning S, Parsons AJ. The stability of grazing systems revisited: spatial models and the role of heterogeneity. *Functional Ecology*. 1999; 13: 737-747.

27. Sullivan S, RohdeR. On non-equilibrium in arid and semi-arid grazing systems. *Journal of Biogeography*. 2002; 29: 1595-1618.

28. Swain DL, Hutchings MR, Marion G. Using a spatially explicit model to understand the impact of search rate and search distance on spatial heterogeneity within a grazing system. *Ecological Modelling*. 2007; 203: 319-326.

29. Phillips CJC. *Cattle Behaviour*. Ipswich, United Kingdom: Farming Press Books, 1993.

30. Lazo A, Soriguer RC. Size-Biased Foraging Behavior in Feral Cattle. *Applied Animal Behaviour Science*. 1993; 36: 99-110.

31. Marion G, *et al*. Application, analysis and parameter estimation in agent-based models of foraging behaviour in spatially heterogeneous systems. *Journal of Agricultural Science* . In press.

32. Hutchings MR, *et al*. Grazing in heterogeneous environments: infra- and supra-parasite distributions determine herbivore grazing decisions. *Oecologia*. 2002; 132:453-460.

33. King EJ, Lovell DJ, Harris S. Efect of climate on the survival of *Mycobacterium bovis* and it's transmission to cattle herds in south-west Britain. In: Cowen DP, Feare CJ, eds. *Advances in Vertebrate Pest Management.* Furth, Germany; Filander Verlag, 1999. pp 147-162.

34. Brown JA, Harris S, White PCL. Persistence of *Mycobacterium bovis* in cattle. *Trends in Microbiology*. 1994; 2: 43-46.

35. Daniels MJ, *et al*. Do non-ruminant wildlife pose a risk of paratuberculosis to domestic livestock and vice versa in Scotland? *Journal of wildlife disease*. 2003; 39: 10-15.

36. Gallagher J, Hornwill DM. A selective oleic acid albumin agar medium for the cultivation of *Mycobacterium bovis*. *Journal of Hygiene*, 1977; 79: 155-160.

37. Familton AS, McAnulty RW. Life cycles and developments of nematode parasites of ruminants. In: Barrel G, eds. *Sustainable Control of Internal Parasites in Ruminants*. Lincoln: Lincoln University, 1997: pp 67-79.

38. Bates KM, *et al*. Potential for cross-transmission of *Dictyocaulus viviparus* between cattle and white-tailed deer. *Journal of Wildlife Diseases*. 2000; 36: 774-778.

39. Johnson M, *et al*. *Dictyocaulus* species: cross infection between cattle and red deer. *New Zealand Veterinary Journal*. 2003; 51: 93-98.

Table 1: A comparison of the number of bites/number of investigation from dispersed wildlife faeces (150 patches) relative to the number of bites/investigations from latrine wildlife faeces (1 patch), for both levels of cattle avoidance in the set stock scenario and the rotation grazing scenario.

	Relative No. of bites		Relative No. of investigations	
	No avoidance	High avoidance	No avoidance	High avoidance
Set stock grazing				
Day 1-100				
whole simulation	105.39	132.62	95.41	321.83
Day 1-39				
pre equilibrium	113.62	210.92	95.41	487.99
Day 40-100				
post equilibrium	97.95	119.78	91.44	191.94
Rotation grazing				
Day 1-100				
whole simulation	140.35	151.50	173.45	150.91
Day 1-25				
1st Rotation	139.88	167.42	188.27	161.65
Day 51-75				
2nd Rotation	140.83	147.97	161.45	132.63

Legends for Illustrations

Figure 1 – An overview of the spatially configured model framework. Animals graze in the local patch and search in the local neighbourhood (patches are denoted by circles) defined by the power-law search kernel F(i,j) which weights the sward height at each patch in order to determine the actual movement rate. The shaded patches have the largest weights, F(i,j), which declined with distance from the animals current location at site i.

Figure 2: The mean grass availability of wildlife faecal-contaminated patches with high cattle avoidance, cattle faecal-contaminated patches and clean non-contaminated patches for (A) set stock grazing and (B) rotational grazing systems. Figures are the mean number of bites of forage per 0.5m^2 patch per day averaged over 10 simulations, ± standard deviation. The mean grass availability per type of patch (e.g. wildlife faeces; cattle faeces; clean patch) showed little difference between the treatments in each grazing system and so the values shown are mean number of bites of forage available per 0.5m^2 patch type per day averaged over all the treatments.

Figure 3: Effect of herbivore level of avoidance (μa) on (A) number of bites taken and (B) number of investigations taken by cattle from wildlife faecal contaminated patches (left y-axis) and cattle faecal contaminated patches (right y-axis). μa values represent the initial level of avoidance of cattle to fresh wildlife faecal patches. μa=0 is cattle initially show no avoidance of fresh wildlife faeces. Avoidance increases with increasing μa values up to μa=0.75 which is cattle initially show almost complete of fresh wildlife avoidance. Cattle faecal patches represent faeces in the environment deposited by the

cattle during the simulation. Figures are the mean number of bites/number of investigations from wildlife faecal contaminated patches per day averaged over 10 simulations, +/- standard deviation. Grazing and investigative contacts with cattle faeces showed little difference between treatments and so the values shown are the mean number of contacts with cattle faeces over all the treatments.

Figure. 4: Effect of defecation pattern on (A) number of bites taken and (B) number of investigations taken by cattle from wildlife faecal contaminated patches (left y-axis) and from cattle faecal contaminated patches (right y-axis). 1 contaminated patch is representative of latrine type defecation patterns, and 150 contaminated patches is representative of single dispersed deposit defecation patterns. Cattle faecal patches represent faeces in the environment deposited by the cattle during the simulation. Figures are the mean number of bites/number of investigations from wildlife faecal contaminated patches per day averaged over 10 simulations, +/- standard deviation. Grazing and investigative contacts with cattle faeces showed little difference between treatments and so the values shown are the mean number of contacts with cattle faeces over all the treatments.

Figure 5: Effect of defecation pattern and herbivore level of avoidance in a set stock grazing system, on (A) number of bites taken and (B) number of investigations taken by cattle from wildlife faecal contaminated patches (left y-axis) and from cattle faecal contaminated patches (right y-axis). 1 contaminated patch is representative of latrine type defecation pattern, and 150 contaminated patches is representative of single dispersed

deposit defecation patterns. Cattle faecal patches represent faeces in the environment deposited by the cattle during the simulation Figures are the mean number of bites/number of investigations from wildlife faecal contaminated patches per day averaged over 10 simulations, +/- standard deviation. Grazing and investigative contacts with cattle faeces showed little difference between treatments and so the values shown are the mean number of contacts with cattle faeces over all the treatments.

Figure 6 : Effect of defecation pattern and herbivore level of avoidance in a rotational grazing system, on (A) number of bites taken and (B) number of investigations taken by cattle from faecal contaminated patches. 1 contaminated patch is representative of latrine type defecation pattern, and 150 contaminated patches is representative of single dispersed deposit defecation patterns. Cattle faecal patches represent faeces in the environment deposited by the cattle during the simulation Figures are the mean number of bites/number of investigations from wildlife faecal contaminated patches per day averaged over 10 simulations, +/- standard deviation. Grazing and investigative contacts with cattle faeces showed little difference between treatments and so the values shown are the mean number of contacts with cattle faeces over all the treatments.

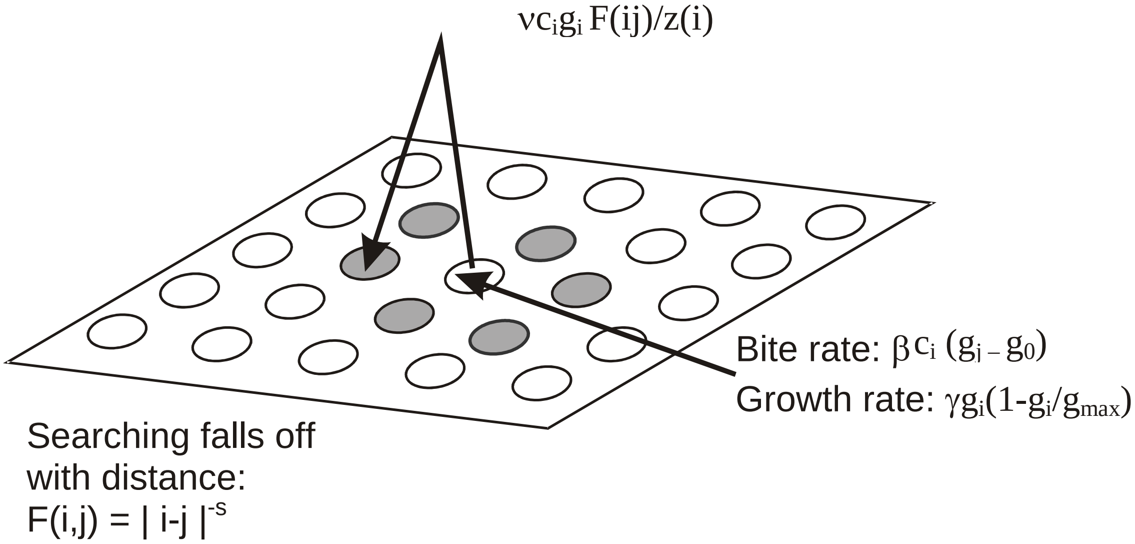

$\nu c_i g_i F(ij)/z(i)$
Bite rate: $\beta c_i (g_{i-} g_0)$
Growth rate: $\gamma g_i(1-g_i/g_{max})$
Searching falls off
with distance:
$F(i,j) = | i-j |^{-s}$

Figure 1

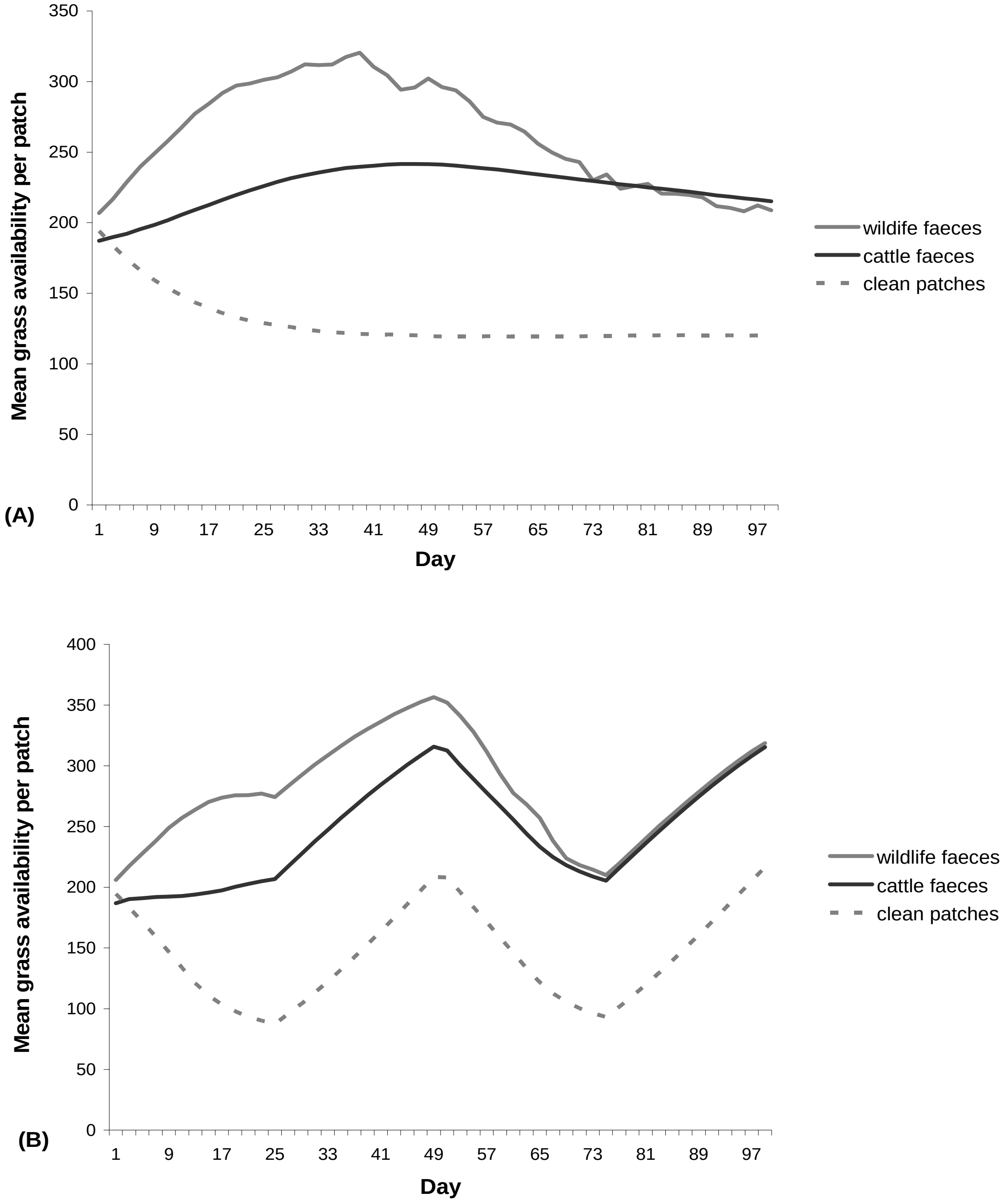

Mean grass availability per patch
350
300
250
200
150
100
50
0
(A)
1
9
17
25
33
41
49
57
65
73
81
89
97
Day
wildife faeces
cattle faeces
clean patches
Mean grass availability per patch
400
350
300
250
200
150
100
50
0
(B)
1
9
17
25
33
41
49
57
65
73
81
89
97
Day
wildlife faeces
cattle faeces
clean patches

Figure 2

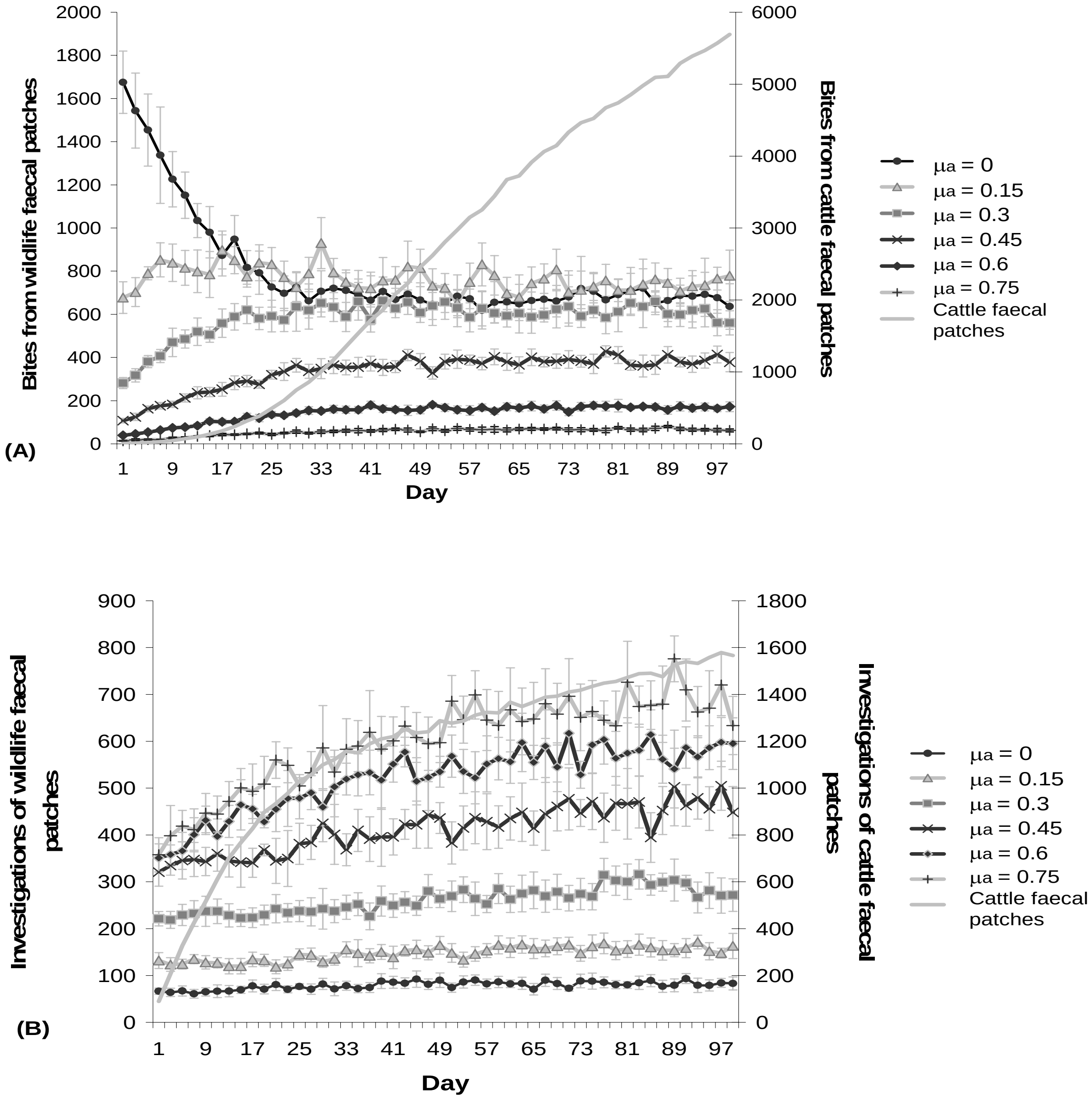
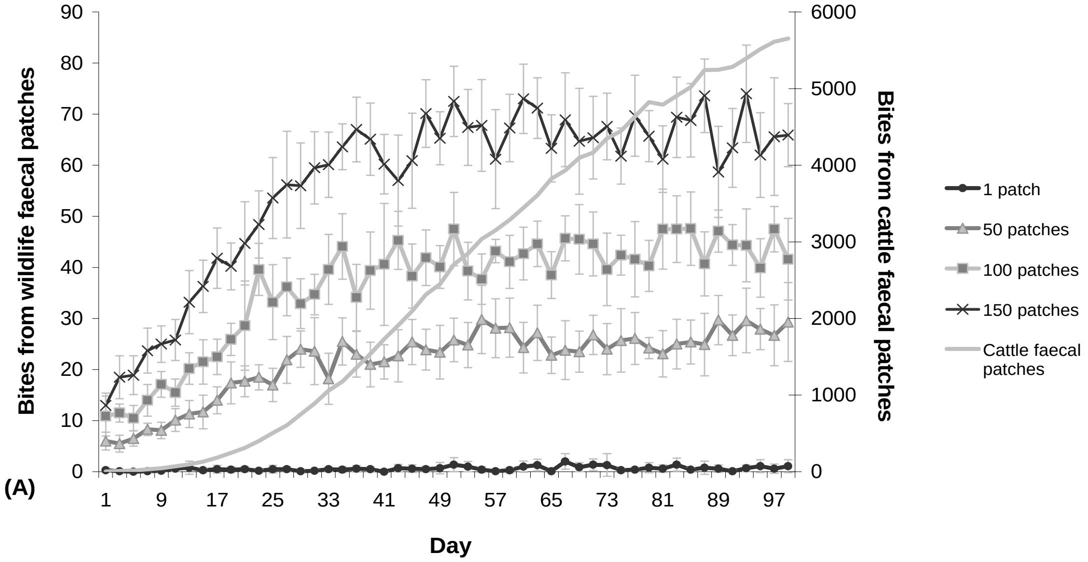
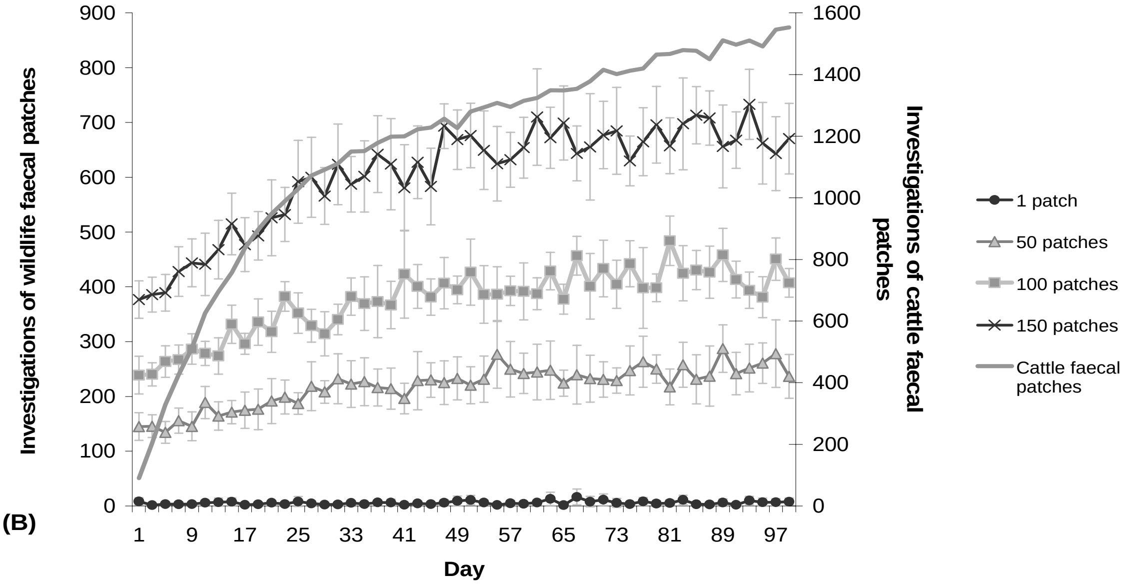

(A)
Bites from wildlife faecal patches
Bites from cattle faecal patches
Day
1
9
17
25
33
41
49
57
65
73
81
89
97
0
200
400
600
800
1000
1200
1400
1600
1800
2000
0
1000
2000
3000
4000
5000
6000
μa = 0
μa = 0.15
μa = 0.3
μa = 0.45
μa = 0.6
μa = 0.75
Cattle faecal patches
(B)
Investigations of wildlife faecal patches
Investigations of cattle faecal patches
Day
0
100
200
300
400
500
600
700
800
900
0
200
400
600
800
1000
1200
1400
1600
1800

Figure 3

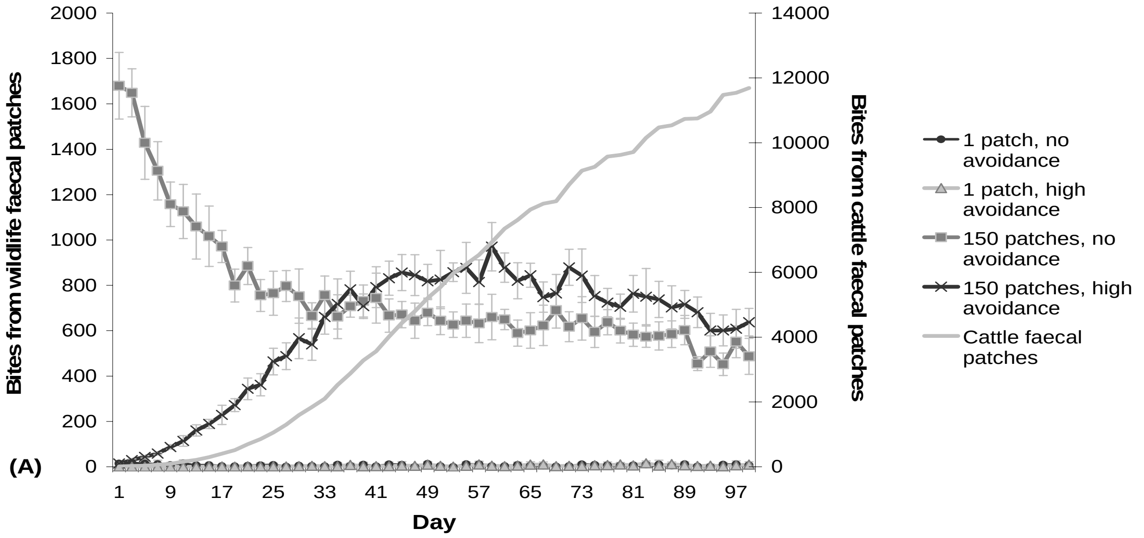


90
80
70
60
50
40
30
20
10
0
Bites from wildlife faecal patches
6000
5000
4000
3000
2000
1000
0
Bites from cattle faecal patches
1 patch
50 patches
100 patches
150 patches
Cattle faecal patches
(A)
1
9
17
25
33
41
49
57
65
73
81
89
97
Day



900
800
700
600
500
400
300
200
100
0
Investigations of wildlife faecal patches
1600
1400
1200
1000
800
600
400
200
0
Investigations of cattle faecal patches
1 patch
50 patches
100 patches
150 patches
Cattle faecal patches
(B)
1
9
17
25
33
41
49
57
65
73
81
89
97
Day

Figure. 4


(A)
Bites from wildlife faecal patches
Bites from cattle faecal patches
Day
0
200
400
600
800
1000
1200
1400
1600
1800
2000
0
2000
4000
6000
8000
10000
12000
14000
1 9 17 25 33 41 49 57 65 73 81 89 97
1 patch, no avoidance
1 patch, high avoidance
150 patches, no avoidance
150 patches, high avoidance
Cattle faecal patches

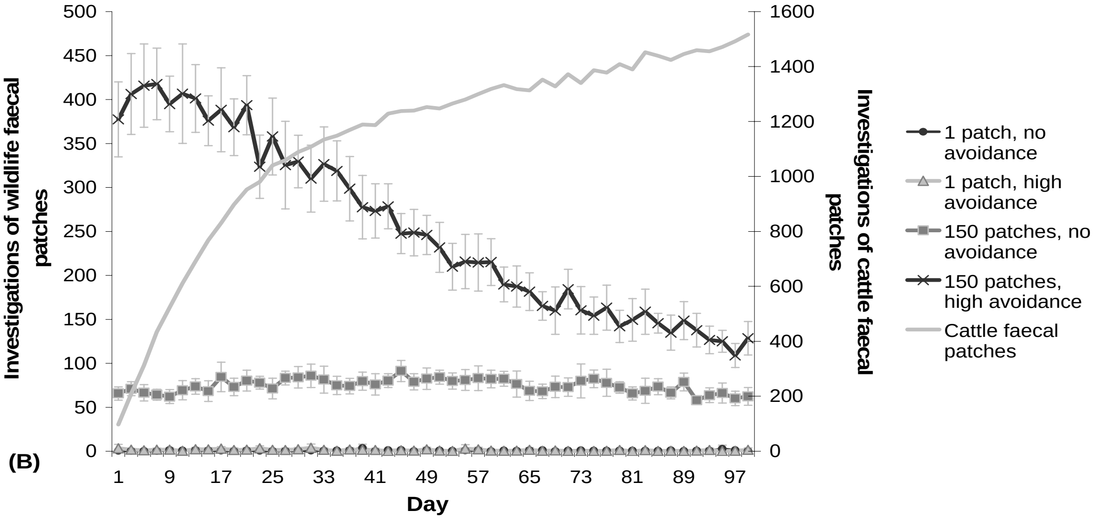

(B)
Investigations of wildlife faecal patches
Investigations of cattle faecal patches
Day
0
50
100
150
200
250
300
350
400
450
500
0
200
400
600
800
1000
1200
1400
1600
1 9 17 25 33 41 49 57 65 73 81 89 97
1 patch, no avoidance
1 patch, high avoidance
150 patches, no avoidance
150 patches, high avoidance
Cattle faecal patches

Figure 5

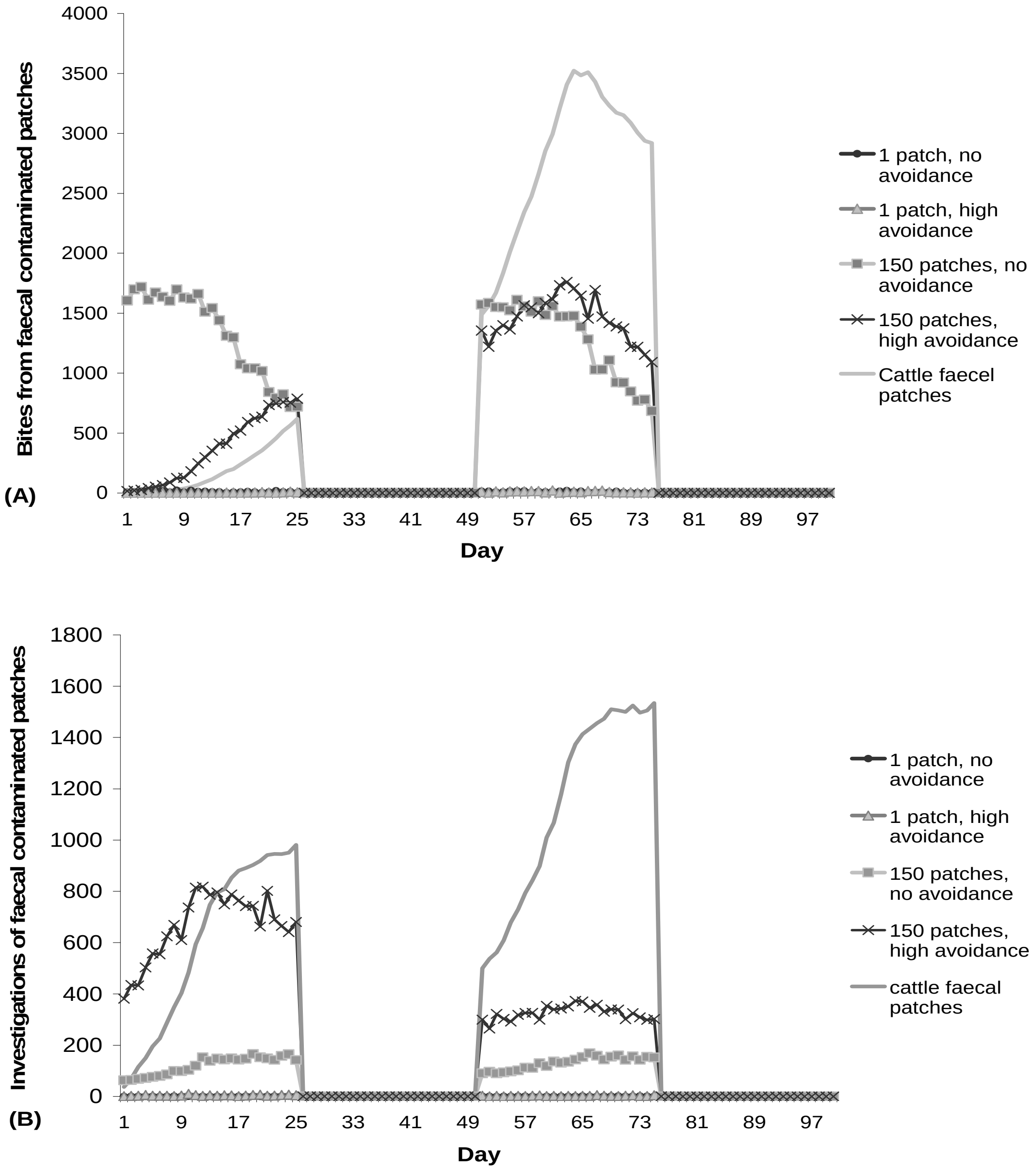

(A)
Bites from faecal contaminated patches
4000
3500
3000
2500
2000
1500
1000
500
0
1
9
17
25
33
41
49
57
65
73
81
89
97
Day
1 patch, no avoidance
1 patch, high avoidance
150 patches, no avoidance
150 patches, high avoidance
Cattle faecel patches
(B)
Investigations of faecal contaminated patches
1800
1600
1400
1200
1000
800
600
400
200
0
1
9
17
25
33
41
49
57
65
73
81
89
97
Day
1 patch, no avoidance
1 patch, high avoidance
150 patches, no avoidance
150 patches, high avoidance
cattle faecal patches

Figure 6