PREVENTIVE VETERINARY MEDICINE
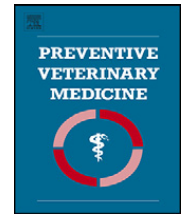
The effect of grazing management on livestock exposure to parasites via the faecal–oral route

L.A. Smith [a,*], G. Marion [b], D.L. Swain [c], P.C.L. White [d], M.R. Hutchings [a]

[a] Animal Nutrition and Health, Scottish Agricultural College, West Mains Road, Edinburgh EH9 3JG, UK
[b] Biomathematics & Statistics Scotland, JCMB, The King's Buildings, Edinburgh EH9 3JZ, UK
[c] CSIRO Livestock Industries, JM Rendel Laboratory, Ibis Avenue, North Rockhampton QLD 4701, UK
[d] Environment Department, University of York, Heslington, York YO10 5DD, UK

ABSTRACT

In grazing systems, heterogeneous distributions of forage resources and faeces result in localised accumulations of nutrients and parasites (both macroparasites and microparasites), creating trade-offs between the costs of exposure to infestation or infection and the benefits of nutrient intake. Each contact between livestock and faeces in the environment is a potential parasite/pathogen transmission event. Thus, herbivores must make foraging decisions in complex environments which will affect their intake of both nutrients and parasites. However, the pattern of forage and faecal resources in agricultural environments will also be affected by the grazing management system in place. The aim of this study was to investigate the effect of grazing management on the risk of infection/infestation to livestock. We used a spatially explicit individual based stochastic foraging model to simulate livestock contact (both grazing and investigative) with faeces in the environment. The model was parameterised to simulate cattle grazing under three types of grazing management: set stock (i.e. where sward growth and cattle intake are in equilibrium in a single field); a two pasture rotation grazing system with increasing number of rotations; and a rotational grazing system with two rotations and increasing subdivisions of the pasture. Overall the amount of cattle contact with faecal-contaminated patches was similar in both set stocking and rotational grazing scenarios, suggesting no difference in the risk of infection or infestation between the different systems. However, the timing and absolute amounts of peak contact varied greatly indicating that different grazing management systems expose livestock to risks of different types of parasites at different times of the grazing season. Intensive rotational systems with small pasture blocks (especially the first grazing period) maximised livestock contact with fresh faeces, and thus exposure to microparasites (e.g. bacterial pathogens). Livestock re-entering pasture blocks in rotational systems and set stocked livestock had the highest contact with old faeces and thus have a greater risk of macroparasite transmission (gastrointestinal nematodes). This study highlights how livestock management affects the highly dynamic interaction between livestock and distributions of parasites in the environment and thus the levels of livestock exposure to parasites and pathogens via the faecal–oral route.

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1. Introduction

Herbivores in natural and agricultural grazing systems will come into contact with faeces whilst they are grazing.

* Corresponding author. Tel.: +44 131 535 3452; fax: +44 131 535 3121.
  E-mail address: lesley.smith@sac.ac.uk (L.A. Smith).

Both macroparasites (e.g. parasitic helminths) and microparasites (e.g. bacterial pathogens) are found in host animal faeces and thus can be transmitted to herbivores via grazing (Sykes, 1987). Pathogen transmission from faecal-contaminated vegetation can occur via two main routes, ingestion of faecal-contaminated vegetation, and investigation of contaminated vegetation. Thus, the behavioural contact pattern of grazing herbivores with faeces in the environment plays an important role in the risk of parasite/pathogen transmission via the faecal–oral route. However, herbivores generally avoid grazing near faeces (Forbes and Hodgson, 1985; Benham and Broom, 1991; Hutchings and Harris, 1997; Bao et al., 1998; Hutchings et al., 1998), and will modify their grazing behaviour to become more selective when forced to graze faecal-contaminated forage (Hutchings et al., 1998) or pasture spread with slurry (Pain et al., 1974; Broom et al., 1975; Pain and Broom, 1978; Swain et al., 2008). This selective grazing behaviour affects the sward structure of the grazing environment creating a heterogeneous landscape of gaps (short, non-contaminated, grazed patches) and tussocks (tall, faeces-contaminated, avoided patches) (Hutchings et al., 2001). Additionally, the faecal deposits contain nutrients that leach into the surrounding area causing tussocks to have increased nutrient content relative to gap swards (Haynes and Williams, 1993). Thus the mosaic represents a nutrition versus parasitism trade-off in that the faeces-contaminated tussocks are localised concentrations of nutritional resources, providing herbivores with up to 32% increased forage intake rate and 41% increased nitrogen content; however tussocks also contain up to 17 times greater numbers of parasites (Hutchings et al., 2007). Herbivores must make grazing decisions based on the costs and benefits of this trade-off, which are affected by both animal factors (e.g. physiological state) and environmental factors (e.g. forage availability) (Hutchings et al., 1999). Thus, in agricultural grazing systems it is the interplay of these factors which will determine the livestock parasite exposure and infection/infestation risk.

Different grazing management systems are used to provide livestock with a supply of herbage whilst effectively utilising the productivity of the pasture (Holmes, 1989). The two grazing systems considered here are continuous set stock grazing and intensive rotational grazing. In a continuous set stock grazing system a group of livestock have access to an area of pasture for the whole grazing season. In contrast, rotational grazing involves dividing the pasture area up into a number of similar-sized paddocks and the livestock are moved in a regular sequence between the paddocks. This rotational grazing practice allows the herbivore to graze almost all the available pasture in a paddock in order to stimulate sward growth during the paddock's rest period, and therefore increase the productivity of the pasture. Furthermore, it has been found that there is less rejection of faecal-contaminated pasture in a rotational grazing system (Benham and Broom, 1991). Herbivore grazing behaviour in relation to faeces and thus parasites and pathogens, has been shown to be affected by the grazing environment (e.g. nutritional environment) (Smith et al., 2006). Thus, it might be expected that grazing management practices may affect the costs and benefits of the nutrition versus parasitism trade-off and consequently the amount of livestock contact with faeces and therefore exposure to parasites and pathogens in the environment.

Livestock (cattle and sheep) grazing abilities and behaviour are well documented through empirical experimentation and observation (Black and Kenney, 1984; Arnold, 1987; Bazely, 1990; Lynch et al., 1992; Phillips, 1993; WallisDeVries et al., 1998; Hutchings et al., 1998). Therefore, it is possible to develop and parameterise mathematical models that capture livestock–parasite interactions that occur via the faecal–oral route. Here we extended a spatially explicit individual-based stochastic model (Marion et al., 2005; Swain et al., 2007) that allows simulation of cattle grazing behaviour and the contact of cattle with faeces. We use this model to determine the impact of set stocking and rotational grazing on cattle's contact with faeces/pathogens in the environment. Specifically, we test the null hypotheses that grazing system will have no effect on the grazing or investigative contact with faecal-contaminated patches.

2. Methods

2.1. Model

We use simulation code implementing an extended version of a grazing model (Marion et al., 2005) that explicitly captures herbivore contact with faecal contamination in grazing systems (i.e. risk of parasite/pathogen transmission via the faecal–oral route), to address our objectives. The model used in this paper extends that described by Marion et al. (2008) which itself builds on an existing framework (Marion et al., 2005; Swain et al., 2007) which primarily addressed issues relating to resource use efficiency. The model (Marion et al., 2005; Swain et al., 2007) is based on a series of empirically observed behavioural rules that are used to capture herbivore grazing behaviour in heterogeneous landscapes: (1) herbivores visually assess local neighbourhood to select tall and/or more nutrient rich swards over short and/or nutrient poor swards (Bazely, 1990); and (2) herbivores select non-contaminated swards over faecal contaminated swards (Hutchings et al., 1998). 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 patch 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. Marion et al. (2008) show the importance of limited information and spatial heterogeneity in assessing infection/infestation risk, introducing the following novel features: (1) wildlife faecal contamination and associated decay and avoidance parameters; (2) a model for faecal deposition by livestock; and (3)
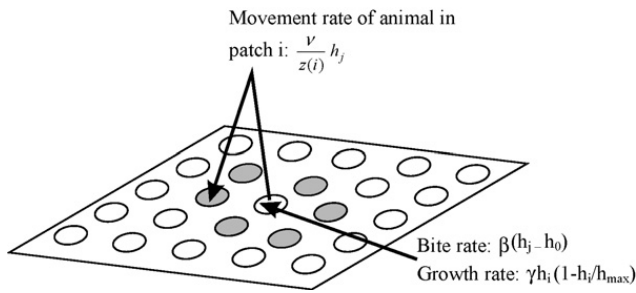
Fig. 1. An overview of the spatially configured model framework. Animals graze in the local patch and search nearest neighbour patches (patches are denoted by circles) only. Where ν is the intrinsic movement rate; $z(i)$ is the number of nearest patches; h_i is the resource available in patch i; h_j is the resource available in patch j; h_0 is the minimum grazable portion each patch; h_{max} is the maximum resource available in each patch; γ is the intrinsic growth rate of the sward. The movement rate weights the sward height of each neighbouring patch and is used to determine the actual movement of individual animals. The bite rate at each patch is linear in the sward height (above the minimum grazable portion h_0) and is reduced exponentially by faecal avoidance $\exp(-\mu_f f_i)$ where μ_f is the level of herbivore avoidance of faeces and f_i level of faecal contamination at patch i. Sward growth at each patch is logistic.

measurement of daily grazing and investigative contact rates as indicators of infection/infestation risk. Features such as nearest neighbour search, grass growth, intrinsic bite rate, and avoidance of livestock faeces were introduced in Marion et al. (2005).

The extension and modifications to Marion et al. (2008) that are used here, are as follows. To describe a range of different management practices, such as set stocking and rotation, the model also 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. To prevent unrealistic overgrazing when animals are returned to a pasture with increased sward height and increased clean patch availability (due to faecal decay), we introduce a maximum daily feed intake for the livestock, denoted dR_k for animal k. Within a given day, animal k will continue grazing until the intake accumulated over the current day reaches dR_k, at which point it stops grazing until the following day when this process is repeated. The search distance of herbivores is currently unknown and extremely difficult to measure (Phillips, 1993). However, Marion et al. (2008) demonstrated that in the context of a managed temperate grazing system, such as that considered here, varying the search distance had little effect on model-predicted infection/infestation risk (based on 10 replicate simulations, the single standard deviation confidence intervals in mean risks associated with nearest-neighbour and global searching always overlapped), and therefore here we adopt a nearest neighbour search model.

In addition to the features described in the preceding paragraph the model is as described by Marion et al. (2008), except that here we do not consider wildlife sources of infection or infestation. The model state-space represents, at site i, the sward height h_i, the number of animals c_i, and the faecal contamination f_i due to livestock. In addition s_k represents the stomach contents of animal $k = 1, \ldots, A$, where the total number of animals is

$A = \sum_{i=1}^{N} c_i$. All state variables are assumed to be integers. The sward growth rate in each patch, $i = 1, \ldots, N$, is assumed to be logistic $\gamma\, h_i(1 - h_i/h_{max})$, where γ is the intrinsic (in the absence of density dependence) sward growth rate, and h_{max} is the maximum sward height attainable in the absence of grazing pressure. Individuals were assumed to bite at a rate of

$$\beta(h_i(t) - h_0)e^{-\mu_f f_i} \tag{1}$$

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

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

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 requirement means that the there is a time-lag in the dynamics of the system between intake and faecal deposition.

As described in Marion et al. (2005), we assume nearest neighbour searching at rate

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

for each animal at patch i, the $z(i)$ (usually four except at the edge of the lattice) nearest neighbours of site i denoted as $j \in N_i$, where ν is the intrinsic search, or movement rate.

The events and event rates are summarised in Table 1, and subsequently this model is simulated as a stochastic (discrete state-space Markov process) model in which during a given small time interval from t up to $t + \delta t$, written as $(t, t + \delta t)$, an event of type x with associated rate r_x occurs with probability $r_x\, \delta t$. The total event rate $R = \sum_x r_x$ is given by summing the bite, movement and deposition rates in Table 1 across all animals, and the growth and faecal decay rates over all patches. The time-step δt is then chosen such that $R\delta t < 1$ (i.e. all the terms $r_x\, \delta t < 1$ can be interpreted as probabilities). For example, see Renshaw (1991) for an introduction to Markov process modelling and simulation of biological populations, and Marion et al. (2008) for a more detailed description of the above algorithm.

2.2. Parameterisation

The model was parameterised to simulate three cattle grazing under three types of grazing management: set stock (i.e. where sward growth and cattle intake are in equilibrium in a single field); a two pasture rotation grazing system with increasing number of rotations; and a rotational grazing system with two rotations and increasing subdivisions of the pasture. Each grazing system was represented by a lattice of patches. It was important to ensure the simulations replicated the spatial scale of

Table 1

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

Event description	Change in state space					Event rate at time t
	δh_i	$\delta i(k)$	δs_k	δw_i	δf_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	$\beta(h_i - h_0)^* \exp(-\mu_f f_i)$
Movement of animal k from current patch $i(k)$ to nearest neighbour patch j	0	$i(k) \rightarrow j$	0	0	0	$\frac{\nu}{z(i)} c_i h_j$
Faecal deposition at current patch $i = i(k)$	0	0	$-s_0$	0	$+s_0$	$(s_k - s_0) f_{dep} \times \Theta(s_k - s_0)$
Decay of livestock faecal contamination at patch i	0	0	0	0	−1	$\lambda_f f_i$

agricultural systems as parasite/pathogen transmission occurs on a bite by bite basis. Thus, each patch represented 0.5 m^2, the approximate area of one cattle faecal pat and the rejected area around it (Phillips, 1993). The resources in each patch are defined as the number of bites available per patch. Each cattle bite is approximately 0.001 m^2 (Phillips, 1993), thus the 0.5 m^2 patch used in these simulations contains a minimum of 50 bites of forage resources. This represents the ungrazable portion of each patch. However, each patch starts with an initial sward height (h_0) of 200 bites of forage resources per patch; and has a maximum sward height (h_{max}) of 400 bites per patch.

2.2.1. Set stock grazing

The set stock simulations were carried out with three identically parameterised animals on a 70×70 patch lattice, representing a pasture of 0.25 ha. The simulation size was a compromise between the duration of individual runs of the model, the number of animals and paddock size. The sward growth rate ($\gamma = 0.00004$) was calculated to provide a set stock scenario, i.e. where mean grass height is stable and sward growth is equal to herbivore intake, where herbivore grazing rate (β) represented approximately 30000 bites of herbage a day ($\beta = 0.1$) (Phillips, 1993) and a herbivore movement rate (ν) represent a cattle step rate of approximately 3 steps a minute (Lazo and Soriguer, 1993) ($\nu = 0.015$). To enable a comparison of the number of bites from faecal-contaminated patches between the different grazing systems (set stock and rotation grazing) each individual cattle's daily intake requirement was restricted to the average individual cattle intake when unrestricted in a set stock environment ($dR_k = 9000$). The search distance of herbivores in pastoral environments is currently unknown, and it may be expected to influence levels of contact between herbivores and faeces in the environment. However, the sensitivity of the model to changes in the search distance was tested, and it was found that due to the high movement rate of grazing cattle in the small field sizes such as those used in agricultural systems, the frequency of cattle contact with faeces is insensitive to search distance (Marion et al., 2008). As a result, searching was restricted to next-nearest neighbour. At the start of the simulation, cattle were introduced onto a pasture free of any cattle faecal contamination ($f_i = 0 \ \forall i = 1, \ldots, N$) and cattle deposited

faeces approximately 10–15 times a day (Phillips, 1993) ($f_{dep} = 1.0$, $s_0 = 2000.0$). Cattle faeces had a decay rate, where degradation to approximately 10% of the initial faecal deposit would occur 3 months after deposition (Haynes and Williams, 1993) ($\lambda_f = 0.00001776$). Initial response by cattle to a deposit of their own fresh faeces was set at almost complete avoidance (Forbes and Hodgson, 1985) ($\mu_f = 0.0025$, corresponding to a bite rate from freshly faecal-contaminate patches of less than one percent of the bite rate from clean patches). All the simulations were run for 160 days (i.e. approximate 6 month grazing year).

2.2.2. Two pasture rotational grazing

A two pasture rotational grazing system was captured by simulating one of the pastures during the grazing periods (when cattle were present on the pasture) and during the rest periods (when cattle were absent but sward growth and faecal decay in the pasture continued). The simulated pasture was half the size of the set stock pasture, thus the simulations were carried out on a 49×50 patch lattice, representing a pasture of 0.125 ha. Four different rotation scenarios were simulated by increasing the number of times the cattle were rotated into the simulated pasture within a fixed 160 day time-frame. Thus the cattle were rotated in to the simulated pasture for two, three, four and five rotations, with a grazing period of 40, 26.67, 20 and 16 days respectively. All other parameters were the same as the set stock scenario.

2.2.3. Rotational grazing with two rotations

To simulate a rotational grazing system with two rotations, five different rotation scenarios were simulated with increasing subdivisions of the pasture, and the cattle were rotated round each pasture twice. As with the two pasture grazing, only one of the pastures was simulated for each simulation and the size of that pasture was determined by dividing the set stock pasture by the number of pastures in the rotational grazing system, so that the total pastures in the system represented 0.25 ha. Thus, the cattle were rotated twice round 2, 4, 8, 16 and 32 pastures in the rotational grazing system, with a grazing period in the modelled portion of the pasture of 40, 20, 10, 5 and 2.5 days respectively. All other parameters were the same as the set stock scenario.

2.3. Measurements from each grazing scenario

The following grazing statistics (model outputs) were gathered for each scenario described above.

1. The mean forage availability (number of bites available per 0.5 m² patch) of faecal contaminated patches.
2. The mean forage availability of clean patches.
3. The number of bites from faecal-contaminated patches per day.
4. The number of investigations from faecal contaminated patches per day. An investigation was defined as a visit to a patch with no bites.
5. The total number of bites (total intake) per day.

Due to pasture restriction in the rotational grazing systems, the total number of bites per day differed between grazing scenarios, so the number of bites from faecal-contaminated patches are presented as the mean proportion of the total bites per day. Each scenario described was repeated over 10 simulations and we report the estimated expectation value and the standard error in this estimate for each of the quantities described above. The results show this rather modest number of simulations was adequate to reduce these estimation errors to acceptably small levels, and more accurate estimations from a greater number of simulations would not change the conclusions drawn from the results.

3. Results

3.1. Forage availability in the grazing systems

Overall the mean number of bites of forage available in a 0.5 m² patch of faecal-contaminated patches was greater than the mean number of bites of forage available in a 0.5 m² patch of clean non-contaminated patches in all grazing systems (Figs. 2 and 3). In the set stock grazing system there was an increase in the forage availability of faecal-contaminated patches until approximately day 50, after which grazing reduced the amount of forage available in the faecal-contaminated patches. In contrast, the forage availability of clean non-contaminated patches continued to decline over the course of the whole 160 days (Figs. 2 and 3). Thus in the set stock system, at the maximum difference in forage availability, faecal-contaminated patches had 1.95 times greater available forage compared to the non-contaminated clean patches. In the rotational grazing systems there was an even greater difference in the forage availability between the faecal-contaminated patches and the non-contaminated patches. In all rotational scenarios, during the first rotation there was a decline in the mean forage availability of clean non-contaminated patches. However, the mean forage availability of the faecal-contaminated patches during the first rotation varied depending on the number of pasture blocks in the system and thus size of the pasture blocks. In the two pasture rotation system, where the pasture blocks simulated had the greatest area, the mean forage availability of faecal-contaminated patches remained constant. At the maximum difference in forage availability, faecal-

contaminated patches had 4.9 times greater available forage compared to the non-contaminated clean patches (Fig. 2A). In contrast, when there was a decrease in size of each pasture block (i.e. the system was divided into a greater number of pasture blocks), there was a decrease in the mean forage availability of the non-contaminated patches. Thus, the maximum difference in availability between faecal-contaminated and non-contaminated patches occurred in the system with the greatest number of pasture blocks and thus smallest size of each block, e.g. the faecal-contaminated patches had 7.34 times greater available forage compared to the non-contaminated clean patches (Fig. 3A). The difference in forage availability between the faecal-contaminated patches and the clean non-contaminated patches declined with each subsequent rotation. For all the rotational grazing systems, there was an increase in mean forage availability of both faecal-contaminated patches (Figs. 2A and 3A) and clean non-contaminated patches (Figs. 2B and 3B) during the rest period, when the cattle were absent from the pasture. When cattle are rotated back on to the pasture there was an immediate depletion in mean forage availability of faecal-contaminated patches (Figs. 2A and 3A) and clean non-contaminated patches (Figs. 2B and 3B). This pattern of grass growth and depletion was then repeated for each subsequent rotation (Figs. 2 and 3).

3.2. Cattle grazing and investigative contact of faecal-contaminated patches

In all the scenarios considered there were few bites from faecal-contaminated patches relative to the total number of bites per day, with the maximum proportion of bites being 0.35. The patterns of cattle grazing and investigative contact with faecal-contaminated patches were similar. For set stock grazing there was an increase in the mean proportion of bites (Fig. 4A and B) and the mean number of investigations (Fig. 5A and B) from faecal-contaminated patches per day, with increasing time spent on pasture. Similarly, for all rotation grazing scenarios there was an increase in the proportion of bites (Fig. 4A and B) and the mean number of investigations (Fig. 5A and B) from faecal-contaminated patches, with increasing time during each rotation. The maximum proportion of bites (Fig. 4A and B) and number of investigations (Fig. 3A and B) from contaminated patches during each rotation was greater in the rotational grazing scenarios relative to the same grazing period for the set stock grazing scenario. Furthermore, in the rotational grazing scenarios, the maximum proportion of bites (Fig. 4A and B) and the maximum number of investigations (Fig. 5A and B) increased with each subsequent rotation.

The overall mean proportion of bites and the overall mean number of investigations per day taken from faecal-contaminated patches in both types of rotational grazing systems was relatively similar to the set stock grazing system. However, there was a lower proportion of bites per day relative to set stock in rotational systems with more than two subdivisions of pasture (Table 2). The mean proportion of bites and mean number of investigations per day were not consistent across the rotations. In the first
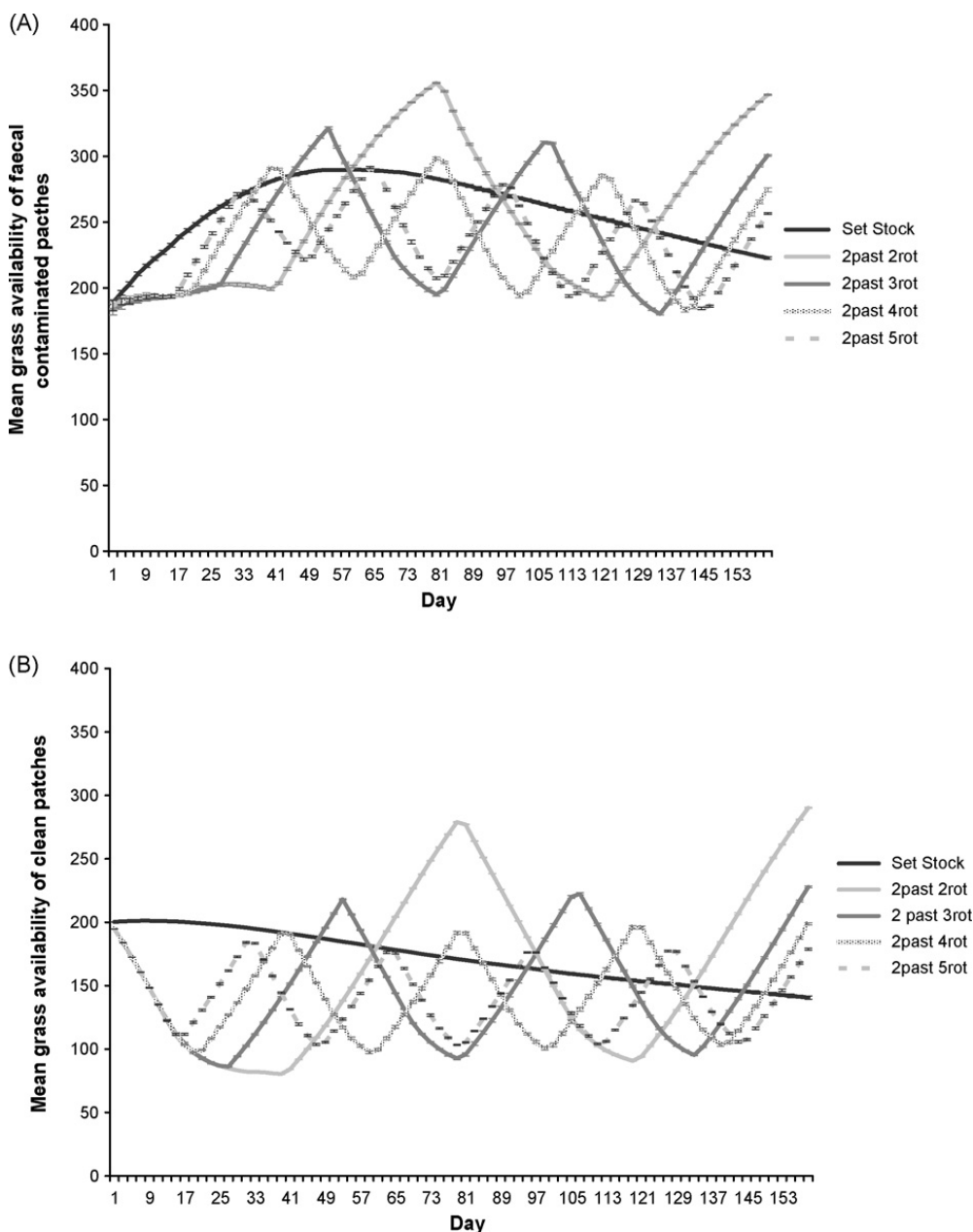
Fig. 2. Effect of set stock versus the two pasture rotation system with an increasing number of rotations on (A) the mean grass availability of faecal contaminated patches and (B) the mean availability of clean patches. Figures are the mean number of bites of forage per 0.5 m² patch per day averaged over 10 simulations, ±standard deviation. Set stock is where cattle remain in the one pasture for the whole grazing scenario. All the rotation scenarios were simulated on 2 pastures that were half the size of the set stock pasture. 2 past 2 rot is a rotation grazing scenario where cattle are rotated round the two pastures twice. 2 past 3 rot is a rotation grazing scenario where cattle are rotated round the two pastures three times. 2 past 4 rot is a rotation grazing scenario where cattle are rotated round the two pastures, four times. 2 past 5 rot is a rotation grazing scenario where cattle are rotated round the two pastures five times.

rotation there were a greater mean proportion of bites and mean number of investigations per day in all the rotation grazing systems relative to the set stock grazing system, with the rotational grazing system with two rotations and increasing subdivisions of pasture having the greatest grazing and investigative contact relative to the set stock grazing system (Table 2). During the first rotation of the two pasture rotational grazing systems, the proportion of bites relative to set stocking increased with increasing number of days per rotation. For example, when there were five rotations and the duration of each rotation was 16 days, the mean proportion of bites was only 4.43 times

greater than the set stock system. When the two pasture rotation system only had two rotations and the duration of each rotation was 40 days, the mean proportion of bites was 8.64 times greater than the set stock system (Table 2). During the first rotation of the grazing systems with two rotations, the proportion of bites relative to set stocking increased with the greater number of pastures in the system. For example, when there were only two pastures, the mean proportion of bites was only 8.64 times greater than the set stock system. However, the proportion of bites increased up to 232 times greater than the set stock system in the 32-pasture system (Table 2). During the first
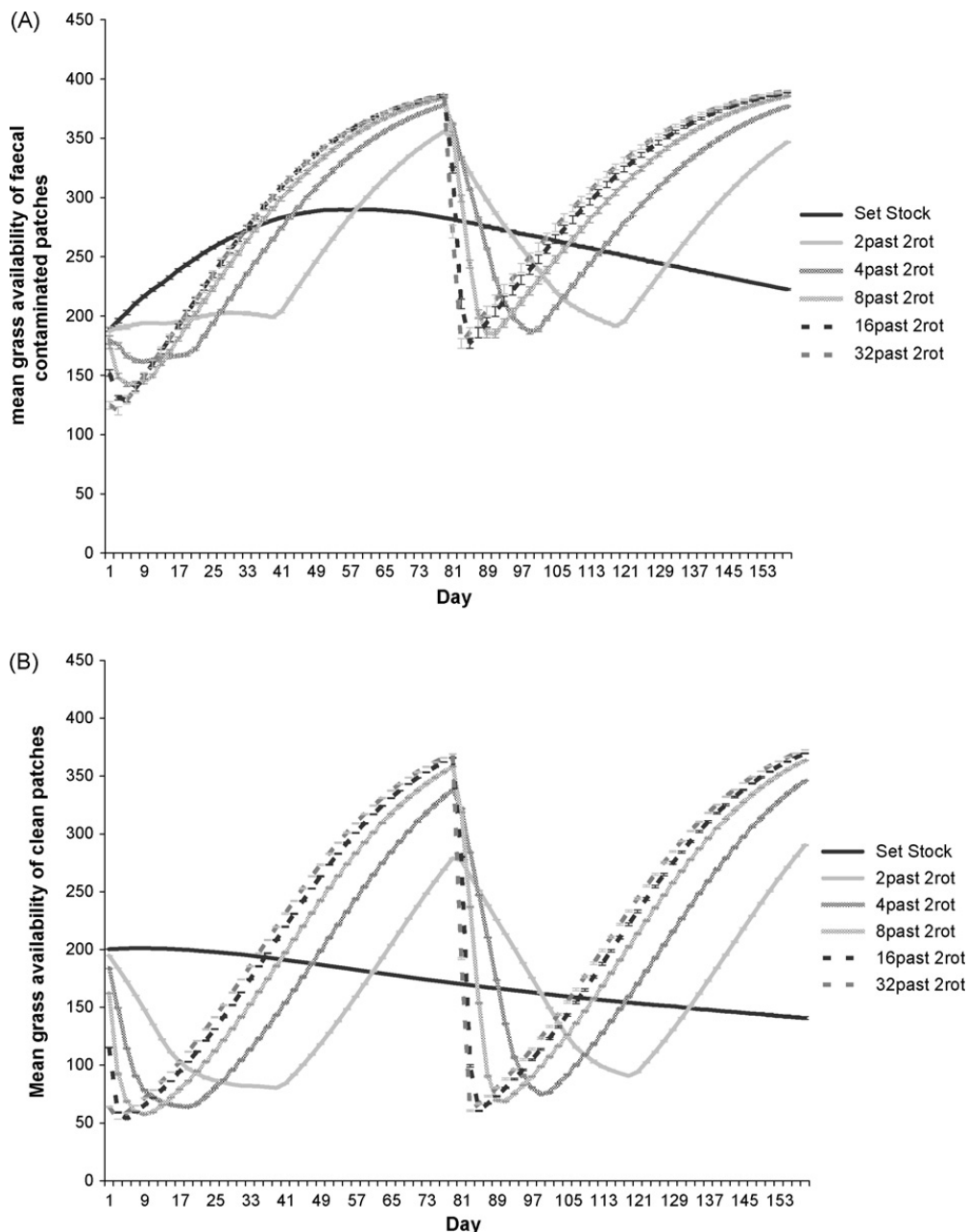
Fig. 3. Effect of set stock versus the rotational grazing system with two rotations and increasing subdivisions of pasture, on (A) the mean grass availability of faecal contaminated patches and (B) the mean availability of clean patches. Figures are the mean number of bites of forage per 0.5 m² patch per day averaged over 10 simulations, ±standard deviation. Set stock is where cattle remain in the one pasture for the whole grazing scenario. In all the rotation scenarios, cattle are rotated round all the pastures twice. Each rotation pasture was the size of the set stock pasture divided by the number of pastures in the rotation grazing system. 2 past 2 rot is a rotation grazing scenario the cattle are rotated round two pastures. 4 past 2 rot is a rotation grazing scenario where cattle are rotated round four pastures. 8 past 2 rot is a rotation grazing scenario where cattle are rotated round eight pastures. 16 past 2 rot is a rotation grazing scenario where cattle are rotated round sixteen pastures. 32 past 2 rot is a rotation grazing scenario where cattle are rotated round 32 pastures.

rotation, the level of investigative contact with faecal contaminated patches in the two pasture rotations system is approximately 2–2.5 times greater than the set stock grazing system. However, in the rotational grazing system with two rotations and increasing subdivisions of pasture, there was an increase in the number of investigations per day relative to set stock grazing, with decreasing pasture size (Table 2). In subsequent rotations, the mean proportion of bites and the mean number of investigations in rotational grazing systems were similar to levels in the set stock grazing system (Table 2).

4. Discussion

The aim of this study was to determine how grazing systems affect cattle grazing behaviour in relation to environmental distributions of forage resources and faeces/parasites. In agricultural systems, cattle will deposit faeces onto the pasture daily and must make foraging decisions in faecal contaminated environments. Cattle strongly avoid their own faeces and those of other species (Smith et al., 2009) creating a heterogeneous gap and tussock mosaic (Hutchings et al., 2001). The first step in this study
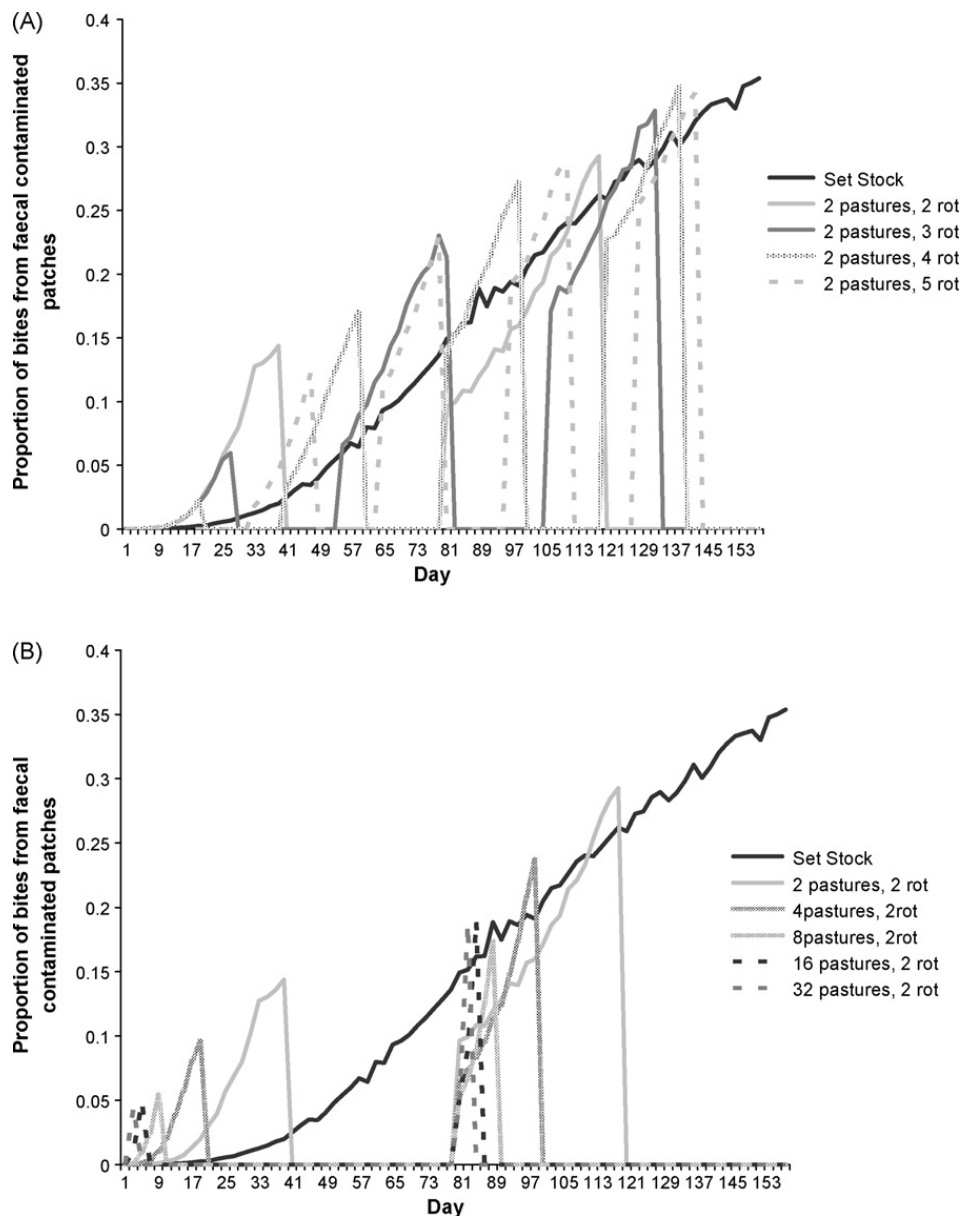
Fig. 4. Effect of set stock grazing versus two types of rotational grazing systems, (A) a two pasture rotation grazing system with increasing number of rotations and (B) a rotational grazing system with two rotations and increasing number of rotations, on the proportion of bites taken from faecal-contaminated patches. Figures are the mean number of cattle bites from faecal contaminated patches per day as a proportion of the mean animal intake per day. All figures are averaged over 10 simulations. Set stock is the where cattle remain in the one pasture for the whole grazing scenario. In (A) all the rotation scenarios were simulated on 2 pastures, which were half the size of the set stock pasture. 2 past 2 rot is a rotation grazing scenario where cattle are rotated round the two pastures twice. 2 past 3 rot is a rotation grazing scenario where cattle are rotated round the two pastures three times. 2 past 4 rot is a rotation grazing scenario where cattle are rotated round the two pastures, four times. 2 past 5 rot is a rotation scenario where cattle are rotated round the two pastures five times. In (B) the cattle are rotated round all the pastures twice. Each rotation pasture was the size of the set stock pasture divided by the number of pastures in the rotation grazing system. 2 past 2 rot is a rotation grazing scenario the cattle are rotated round two pastures. 4 past 2 rot is a rotation grazing scenario where cattle are rotated round four pastures. 8 past 2 rot is a rotation grazing scenario where cattle are rotated round eight pastures. 16 past 2 rot is a rotation grazing scenario where cattle are rotated round sixteen pastures. 32 past 2 rot is a rotation grazing scenario where cattle are rotated round 32 pastures.

was to determine if the model successfully simulated the heterogeneous sward structure representing the nutrition versus parasitism trade-off. In all systems, cattle were introduced on to a pasture free of faecal contamination and with a homogenous sward structure. Within a few days of introducing cattle into the system, faecal-contaminated patches in all the grazing systems had significantly greater mean forage availability (i.e. sward height) relative to the clean non-contaminated patches. Thus a heterogeneous sward structure had been created in all the grazing systems,

suggesting that the behavioural rules of grazing herbivores in the model were adequate at creating empirically observed environments, i.e. the emergent properties of the model match empirical observation (Hutchings et al., 2001). Furthermore, the costs and benefits of this dynamic system were also similar to actual systems in that faecal-contaminated patches provide localised concentrations of both nutritional resources and parasites. It should be noted for the simulations presented here, we have limited ourselves to considering vegetative grazing systems which did not
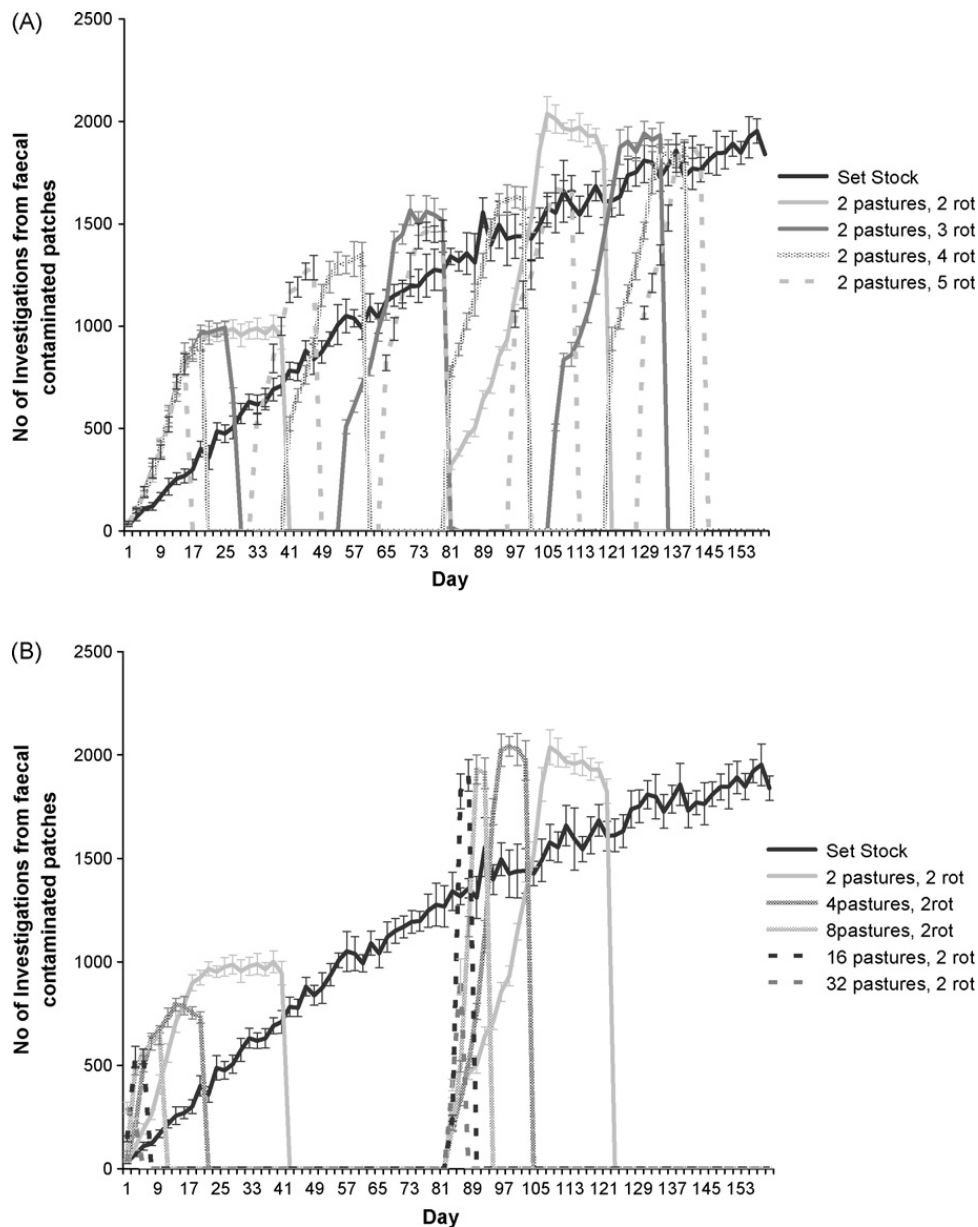
Fig. 5. Effect of set stock grazing versus two types of rotational grazing systems, (A) a two pasture rotation grazing system with increasing number of rotations and (B) a rotational grazing system with two rotations and increasing number of rotations, on the number of investigations of faecal-contaminated patches. Figures are the mean number of investigations from faecal contaminated patches per day, ±standard deviation. All figures are average over 10 simulations. Set stock is the where cattle remain in the one pasture for the whole grazing scenario. In (A) all the rotation scenarios were simulated on 2 pastures, that were half the size of the set stock pasture. 2 past 2 rot is a rotation grazing scenario where cattle are rotated round the two pastures twice. 2 past 3 rot is a rotation grazing scenario where cattle are rotated round the two pastures three times. 2 past 4 rot is a rotation grazing scenario where cattle are rotated round the two pastures, four times. 2 past 5 rot is a rotation scenario where cattle are rotated round the two pastures five times. In (B) the cattle are rotated round all the pastures twice. Each rotation pasture was the size of the set stock pasture divided by the number of pastures in the rotation grazing system. 2 past 2 rot is a rotation grazing scenario the cattle are rotated round two pastures. 4 past 2 rot is a rotation grazing scenario where cattle are rotated round four pastures. 8 past 2 rot is a rotation grazing scenario where cattle are rotated round eight pastures. 16 past 2 rot is a rotation grazing scenario where cattle are rotated round sixteen pastures. 32 past 2 rot is a rotation grazing scenario where cattle are rotated round 32 pastures.

include detailed grass growth staged, e.g. reproduct-ive swards which are less palatable to grazing herbivores.

All cattle in the simulations maintained a degree of avoidance of the faecal-contaminated patches, with relatively few bites taken from faecal-contaminated patches relative to the overall number of bites per day. However, in terms of parasite/pathogen transmission, each contact of a susceptible host with faeces (e.g. a bite/investigation) represents potential exposure to a pathogen. Therefore, the contact behaviours observed here represent

the risk of parasite/pathogen transmission to livestock under the different management systems. Over the whole length of the simulations, the amount of grazing and investigative contact with faecal-contaminated patches was similar for both set stock grazing and all the rotational grazing scenarios modelled. This suggested that there was no difference in the risk of infection or infestation between the different systems. However, when pasture becomes limiting, grazing livestock can be forced to graze faecal-contaminated vegetation (Hutchings et al., 1989), and this

Table 2
A comparison of the mean proportion of bites and number of investigations per day in the rotational grazing scenarios relative to the mean proportion of bites and number of investigations per day for the same grazing period in the set stock scenario. Grazing period is the period of rotation grazing that is being compared to that period of time in the set stock grazing. Number of pastures is the number of pastures that have been simulated for the rotation grazing. Number of rotations in the number of times the cattle have been rotated round all pastures in the rotation grazing scenario.

Grazing period	No of Pastures	No of Rotations	Mean proportion of bites per day relative to set stock	Mean number of investigations per day relative to set stock
All	2 pastures	2 rotations	1.10	1.11
	2 pastures	3 rotations	1.14	1.02
	2 pastures	4 rotations	1.16	1.04
	2 pastures	5 rotations	1.18	0.92
	4 pastures	2 rotations	0.96	1.19
	8 pastures	2 rotations	0.81	1.17
	16 pastures	2 rotations	0.82	1.28
	32 pastures	2 rotations	0.87	1.00
1st Rotation	2 pastures	2 rotations	8.64	1.93
	2 pastures	3 rotations	8.54	2.33
	2 pastures	4 rotations	6.37	2.52
	2 pastures	5 rotations	4.43	2.52
	4 pastures	2 rotations	36.05	2.95
	8 pastures	2 rotations	128.79	4.23
	16 pastures	2 rotations	172.05	6.55
	32 pastures	2 rotations	232.67	6.36
2nd Rotation	2 pastures	2 rotations	0.88	0.90
	2 pastures	3 rotations	1.47	0.98
	2 pastures	4 rotations	2.14	1.16
	2 pastures	5 rotations	2.63	2.48
	4 pastures	2 rotations	0.78	0.93
	8 pastures	2 rotations	0.68	0.90
	16 pastures	2 rotations	0.70	0.99
	32 pastures	2 rotations	0.74	0.80
3rd rotation	2 pastures	3 rotations	0.96	0.85
	2 pastures	4 rotations	1.17	0.94
	2 pastures	5 rotations	1.46	1.06
4th Rotation	2 pastures	4 rotations	0.98	0.88
	2 pastures	5 rotations	1.11	0.95
5th Rotation	2 pastures	5 rotations	1.00	0.90

is reflected in the cattle's investigative and grazing behaviour of faecal-contaminated patches at different periods of grazing under the different grazing systems.

The increased contact with faecal-contaminated patches that occurs in both set stock and rotational grazing systems with increased time on pasture can be attributed to the decline in clean patches with time (i.e. due to continued defecation into the system). Furthermore, when cattle are first placed on the pasture there is an initial strong avoidance of the faecal patches, which results in these patches becoming relatively tall and attractive to cattle compared to the clean patches. This drives the observed initial increase in investigative contact when cattle are first placed on pasture. Decomposition of faeces over time then results in a reduction in avoidance of faeces (Hutchings et al., 1998) resulting in the increase in grazing contact in all grazing systems. 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 infestation (Familton and McAnulty, 1997). Thus, systems where cattle remain on the same pasture for a greater length of time (e.g. set stock grazing or rotational systems with a longer rotation length) increase cattle contact with older faeces and represent a greater risk of macroparasite (e.g. gastrointestinal nematodes) transmission.

The rotation grazing scenarios have increased stocking density relative to the set stock scenarios. This resulted in an increase in grazing and investigative contact during the first period in rotational grazing, relative to the same time period in the set stock scenarios. Thus, when cattle are initially grazed, rotational grazing systems will have a greater proportion of faecal-contaminated pasture (on an area basis) compared to set stock systems and cattle will be forced to graze faecal-contaminated patches sooner. This is consistent with studies that have suggested that farm management practices that reduce pasture availability increase livestock contact with faeces in the environment (Benham and Broom, 1991; Hutchings and Harris, 1997). Microparasite numbers (e.g. *Mycobacterium*) are at their maximum and pose the greatest infection risk when faeces are first deposited in the environment (King et al., 1999). Therefore, during the first grazing period of the rotational cycle in which cattle have more contact with fresh faeces, there is a greater risk of microparasite transmission relative to set stock grazing. The risk associated with this grazing period varies depending on the number of subdivisions of pasture (e.g. pasture size) and length of time for each rotation. In the two-pasture rotational grazing systems cattle increased their grazing contact with faecal-contaminated patches, relative to their grazing contact in set stock

systems, the longer the length of the grazing period. Additionally, increased grazing periods resulted in cattle contacting older faeces and in instances where the grazing periods are greater than several weeks, this will result in not only a greater risk of infection by microparasites but also a greater risk of macroparasite transmission. However, the rotational grazing systems that pose the greatest contact with faeces are those systems that have a larger number of subdivisions of pasture and therefore a smaller pasture size for each rotation cycle. In these systems, changes to the sward structure can be rapid and the clean non-contaminated patches are depleted until they reach the minimum grazable portion. This results in increased grazing contact with faecal-contaminated patches. This highlights the increased risk associated with rotational grazing systems that operate very high stocking densities. Thus, intensive rotational systems such as daily strip grazing, where animals occupy each subdivision of the paddock at a high stocking density for only one day, increase livestock exposure to fresh faeces and thus microparasites (e.g. *Mycobacterium bovis* and *Mycobacterium avium* subsp. *paratuberculosis*).

In subsequent grazing cycles the contacts with faecal-contaminated patches in rotational and set stock systems return to similar levels. This is due to the sward growth that occurs in pastures during the rest period, resulting in a much greater availability of grass at clean patches than over the same grazing period in the set stock pasture. Therefore, during this grazing period faecal-contaminated patches in the set-stock system provide cattle with an increased nutritional advantage compared to the rotational grazing system and present cattle with a heightened dilemma in terms of the nutrition versus parasitism trade-off. However, during the rest period sward growth also occurs at the faecal-contaminated patches. Additionally, decomposition of the faeces at contaminated patches results in cattle having reduced faecal-avoidance behaviour as they enter the pasture. Therefore any contact with faeces during the first day of the grazing period will be with older decomposing faeces, increasing the risk of macroparasite transmission at this time.

The results of the simulations presented here highlight the potential exposure rate of cattle to faeces in different grazing management systems via the faecal–oral route. However, the potential spread of a disease is determined not only by herbivore contact with any faeces in the environment, but by the contact structure between susceptible individuals and faeces from infected individuals. Predicting infection via the faecal–oral route is further complicated by the relationship between exposure to pathogens and actual transmission events, e.g. infection. Currently, there are no definitive data to describe this relationship. Empirical knowledge of these factors would allow a more accurate quantification of exposure to pathogens/parasites in the environment and would greatly strengthen the predictive power of the model.

5. Conclusion

This study indicates that different grazing management systems expose livestock to risks of different types of parasites at different times of the grazing season. It is important to have an understanding of herbivore foraging behaviour under these different grazing systems in order to manage livestock exposure to the various parasites and pathogens transmitted via the faecal–oral route.

Acknowledgements

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