

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

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1 **SUMMARY**

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

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### 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.

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

1  
2 Herbivore grazing behaviour in relation to faeces is also affected by the grazing  
3 environment (e.g. nutritional environment) [19], therefore grazing management practices  
4 which alter the environment will also affect herbivore contact with faeces. Rotational  
5 grazing, a practice to optimize pasture growth and productivity, involves the rotation of  
6 livestock around a number of paddocks giving each paddock a period of rest for  
7 regrowth. This grazing practice allows the herbivore to graze almost all the available  
8 pasture in order to stimulate sward growth during the rest period. The grazing pressure in  
9 rotational systems is therefore relatively high compared to set stocking where animals  
10 continually graze a set pasture size so that grass growth is approximately equal to animal  
11 intake. Grazing systems in which the forage availability may become limiting can result  
12 in animals being forced to graze faecal-contaminated vegetation and studies have  
13 suggested that livestock in rotational systems have increased parasite loads compared  
14 with set stocking [20, 21]. Furthermore, farm management practices which intensify the  
15 grazing pressure are known to increase livestock contact with badger faeces [6, 22].

16  
17 The risk of disease transmission to livestock is therefore driven by the interplay between  
18 herbivore grazing behaviour, pattern of contamination in the environment and farm  
19 management systems. Here we use a spatially explicit individual-based stochastic model  
20 that allows simulation of beef cattle grazing behaviour in terms of a trade-off between  
21 local visual cues and olfactory cues [23] to determine the impact of these interactions on  
22 herbivore contacts with faeces/pathogens in the environment. The first aim of this paper  
23 | is to simulate the behavioural patterns exhibited by cattle in field experiments (Smith,

1 unpublished observations). The subsequent aims are to use the simulation model to  
2 quantify the impact on cattle contact with faeces in the environment of: (1) different  
3 levels of cattle avoidance of faeces; (2) different faecal defecation patterns of wildlife;  
4 and (3) the interaction of these factors in both set stocking and rotation grazing.

5

## 6 **MATERIALS AND METHODS**

7

### 8 **Model**

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

1 (selection or rejection of a patch) are determined by the relative strength of these cues.

2 The formulation of the model is described below.

3

4 The ordinary differential equation below

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6 
$$\frac{dg}{dt} = \gamma g \left( 1 - \frac{g}{g_{\max}} \right) - \beta c (g - g_0), \quad (1)$$

7

8 is a simple, deterministic and non-spatial description of changes in resource density

9 within a grazing system (Note that equation (1) includes no avoidance behaviour.). Here,

10  $g$  is the average sward height,  $\gamma$  is the intrinsic growth rate of the forage resource,  $g_{\max}$  the

11 maximum sward height attainable,  $c$  the average density of foraging animals and  $\beta$  is

12 the per-capita feeding rate and  $g_0$  represents the ungrazable portion of the sward. In

13 practice, grazing systems are both spatially explicit and subject to stochasticity. The

14 feeding rate is therefore determined by the spatial structure of the sward and the

15 interaction between search rate, search distance and bite rate [25]. Within a non-spatial

16 deterministic model such as (1), mediation and maintenance of the grazing system can be

17 achieved through changes in stocking density and or forage growth rate [26].

18

19 Here we formulate an analogous spatially explicit and stochastic model on a unit lattice

20 (i.e. unit spacing between points) of  $N$  patches (indexed by  $i=1, \dots, N$ ) by extending the

21 state-space to represent the sward height  $g_i$  and the number of animals  $c_i$  at patch  $i$ . The

1 total number of animals is  $N_a$ . The probability of an animal grazing in its current patch  
 2 (denoted  $i$ ), during a small time interval  $(t, t + \delta t)$  is

3

$$4 \quad \mathbf{P}(g_i(t + \delta t) = g_i(t) - 1) = \beta c_i(t)(g_i(t) - g_0)\delta t, \quad (2)$$

5

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

14

$$15 \quad \mathbf{P}(g_i(t + \delta t) = (g_i(t) + 1)) = \gamma g_i(t)(1 - g_i/g_{\max})\delta t, \quad (3)$$

16

17 where  $\gamma$  and  $g_{\max}$  are respectively the intrinsic growth rate and maximum sward height.

18 Searching was simulated within a local neighbourhood enabling spatially constrained  
 19 behavioural selection of grazing resources. Searching was described by the probability of  
 20 an animal moving from patch  $i$  to patch  $j$  in a small time interval  $(t, t + \delta t)$  as

$$21 \quad \mathbf{P} \left( \begin{array}{l} c_i(t + \delta t) = c_i(t) - 1 \\ c_j(t + \delta t) = c_j(t) + 1 \end{array} \right) = \frac{v}{z(i)} F(i, j) c_i(t) g_i(t) \delta t \quad \forall j \in N_i, \quad (4)$$



1

2 where  $v$  is the search rate the normalization factor  $z(i)$  was given by

3 
$$z(i) = \sum_{j=1}^N F(i, j) \quad (5)$$

4

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

6 the power-law

7 
$$F(i, j) = |i - j|^{-s} \quad (6)$$

8

9 The normalization factor  $z(i)$  ensures that for large  $s$  (for example  $>10$ ) animals only

10 search nearest neighbouring patches and the model reduces to the original formulation

11 [23] whilst for  $s=0$  the animals search uniformly over the entire arena and the model is

12 closer to the spirit of ref [26]. The characteristic search distance

13

14 
$$d(s) = \exp(\ln(2)/s) \quad (7)$$

15

16 provides a useful description of this power-law search which measures the distance at

17 which the search rate is half that associated with the nearest neighbours (i.e. on the unit

18 lattice patches for which  $|i-j|=1$ ) as a fraction of the distance to the nearest neighbours.

19 Therefore as the power law  $s$  increases, the characteristic search-distance decreases. Note

20 that each of the probabilities (2)-(4) is of the form  $R(n \rightarrow n + \delta n) \delta t$  where the state space is

21 denoted by the vector  $n$  (i.e. a vector containing sward heights  $g_i$  and animal numbers  $c_i$

22 for all patches  $i=1, \dots, N$ ) and the event causing a change  $n \rightarrow n + \delta n$  occurs at rate

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

3

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

5

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

14

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

16 and if it is currently located at patch  $i$  defecation increases the local faecal contamination  
 17  $f_i$  by  $s_0$ .

18

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

$$f_i f_{dk} \tag{10}$$

20

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

$$5 \quad \beta c_i(t)(g_i(t) - g_0) e^{-\mu f_i} \quad (11)$$

6

7 Wildlife faeces are treated as exponentially decaying reservoirs, which are avoided in the  
8 same manner, but to a potentially different extent, as herbivore faeces (Equation 12). In

9 order to explore the effect of avoidance of other faeces, two additional faecal

10 contaminations have been added to the model. At patch  $i$  these contaminations are

11 described by the amount of other faeces from two species, a and b, as  $fa_i$  and

12  $fb_i$  respectively. The deposition of other faeces is not modelled, and from an initial level

13 of contamination (which must be defined), the amount of faeces present is assumed to

14 decay exponentially as before (see equation 10), but with decay rates  $fa_{dk}$  and  $fb_{dk}$ .

15 Avoidance of other faeces is also modelled analogously to the treatment of the

16 herbivore's faeces, but with different levels of avoidance  $\mu_a$  and  $\mu_b$ . Thus the combined

17 effect of all faecal contamination modified the total bite rate across all animals at patch  $i$

18 to

$$19 \quad \beta c_i(t)(g_i(t) - g_0) \exp\left(-\left[\mu f_i + \mu_a fa_i + \mu_b fb_i\right]\right) \quad (12)$$

20

21 An additional feature which was added to the model is the concept of an individual

22 animal's daily intake requirement, denoted  $R_k$  for animal  $k$ . Within a given day, animal  $k$

1 will continue grazing until the intake accumulated over the current day reaches  $R_k$ , at  
2 which point it stops grazing until the following day when this process is repeated.

3

4 To describe a range of different management practices, such as set stocking and rotation,  
5 the model allows the animals to be repeatedly removed and returned to the pasture.

6 | During the periods when the animals are absent from the system, sward growth and faecal  
7 | decay continue as before, but grazing and defecation are suspended. When the animals  
8 | return to the pasture, their accumulated intakes are reset to zero.

9

## 10 **Parameterisation**

11 The model was parameterized to simulate a grazing situation with three beef cows in a  
12 set-stocking scenario, except for the rotational grazing scenario specified below. It was  
13 important to ensure the simulations replicated the spatial scale of agricultural systems as  
14 disease transmission occurs on a bite by bite basis. Thus, all simulations were carried out  
15 in a 70 x 70 patch lattice, where each patch represented  $0.5\text{m}^2$ , the approximate area of  
16 one cattle faecal pat and the rejected area around it [29]. The lattice represented a pasture  
17 of 0.25ha. The simulation size was a compromise between the duration of individual runs  
18 of the model and the number of animals in the system. The set stocking parameters i.e.  
19 where mean grass height is stable and sward growth is equal to herbivore intake (sward  
20 growth rate  $\gamma=0.00004$ ; initial sward height  $g_{\text{start}}=200$ ; maximum sward height  $g_{\text{max}}=400$ )  
21 were calculated from a herbivore grazing rate ( $\beta$ ) that represented approximately 30000  
22 bites of herbage a day ( $\beta = 0.1$ ) [29], and a search rate ( $\nu$ ) that represent a cattle step rate  
23 of approximately 3 steps a min [30] ( $\nu = 0.015$ ). The search distance of herbivores is

1 currently unknown. However, due to the high movement rate of cattle in the relatively  
2 small field sizes used in agricultural systems, cattle contact rates with faeces are  
3 insensitive to search distance [31]. As a result, the search distance coefficient was set to  
4 nearest neighbour ( $s=10$ ), where the grazing herbivore only searches nearest neighbour  
5 patches for all the simulations described. At the start of the simulation, cattle were  
6 introduced into a pasture free of any cattle faecal contamination ( $f_i = 0 \quad \forall i=1, \dots, N$ ) and  
7 cattle deposited faeces approximately 10-15x a day [29] ( $f_{dep} = 1.0$ ,  $s_0=2000.0$ ). Each  
8 individual animal's daily intake requirement was not set, allowing the animals to graze  
9 the whole day. Cattle faeces had a decay rate, where degradation to approximately 10%  
10 of the initial faecal deposit would occur 3 months after deposition [12] ( $f_{dk} =$   
11  $0.00001776$ ). Initial response by cattle to their own fresh faeces was set at almost  
12 complete avoidance [3] ( $\mu=0.0025$ , corresponding to a bite rate from freshly faecal-  
13 contaminate patches of less than one percent of the bite rate from clean patches). In order  
14 to allow a contrast between levels of inter- and intra-specific contact with faeces,  
15 additional faeces were added to the system and were parameterized to represent different  
16 scenarios of wildlife faeces as described in the model runs performed. All the  
17 | simulations were run for 100 days, which, for the set stock scenarios, allowed intake and  
18 | sward heights to reach equilibrium.

19

## 20 **Model runs performed**

21 **Cattle avoidance of wildlife faeces.** To investigate the impact of varying the level of  
22 cattle avoidance of wildlife faeces in isolation, simulations were run with six levels of  
23 cattle avoidance for each patch of wildlife faeces. A herbivore's avoidance level of a

1 patch is dependent on the amount of faeces within it. Thus, in all simulations for cattle  
2 avoidance of wildlife faeces, there were 150 randomly selected patches contaminated  
3 with faeces. Each contaminated patch had 6.67 units of wildlife faeces, giving the same  
4 defecation pattern and the same total amount of wildlife faeces in the environment (1000  
5 units). The avoidance levels simulated were  $\mu_a=0$  (cattle initially show no avoidance of  
6 fresh wildlife faeces, representative of cattle avoidance of rabbit faeces [15]),  $\mu_a=0.15$ ,  
7  $\mu_a=0.3$ ,  $\mu_a=0.45$ ,  $\mu_a=0.6$ ,  $\mu_a=0.75$  (cattle initially show almost complete avoidance of  
8 fresh wildlife faeces, representative of badger faeces [6]). In order to consider cattle  
9 avoidance of wildlife faeces in isolation, all wildlife faeces in the environment were set to  
10 have no decay ( $fa_{dk}=0$ ).

11

12 **Defecation pattern.** To investigate defecation pattern in isolation, simulations were run  
13 with four different defecation patterns with the same total amount of wildlife faeces in the  
14 environment (1000 units), varying the number of contaminated patches. The numbers of  
15 contaminated patches simulated were 1 patch (representative of a latrine type defecation  
16 pattern), 50 patches, 100 patches and 150 patches (representative of single dispersed  
17 deposit defecation patterns). In all cases the contaminated patches were selected at  
18 random. The initial level of avoidance by cattle of each patch contaminated with wildlife  
19 faeces was set to represent ‘almost complete’ avoidance, i.e. the same degree of  
20 avoidance that cattle show towards their own faeces. As a herbivore’s avoidance level of  
21 a patch is dependent on the amount of faeces in the contaminated patch, in order to get  
22 the same initial level of avoidance,  $\mu_a$  varied for each defecation pattern (1 patch,  $\mu_a =$   
23 0.005; 50 patches,  $\mu_a = 0.25$ ; 100 patches,  $\mu_a = 0.5$ ; 150 patches,  $\mu_a = 0.75$ ). To

1 investigate the effect of defecation pattern in isolation, all wildlife faeces in the  
2 environment were set to have no decay ( $fa_{dk} = 0$ ).

3

#### 4 **Interaction between level of avoidance behaviour and wildlife defecation pattern**

##### 5 **(a) Set stock grazing**

6 To investigate the interaction between avoidance level and wildlife defecation pattern  
7 within a set stocking context, four scenarios were modelled with two defecation patterns  
8 (the same total amount of wildlife faeces in the environment (1000 units), varying the  
9 number of contaminated patches) and two levels of cattle avoidance: (1) a single  
10 contaminated patch (representing a latrine-type defecation pattern), with no cattle  
11 avoidance of wildlife faeces ( $\mu_a=0$ ); (2) a single contaminated patch (latrine type  
12 defecation pattern) and almost complete avoidance (for 1 patch contaminated  $\mu_a=0.005$ );  
13 (3) 150 contaminated patches (representing a dispersed defecation pattern) and no cattle  
14 avoidance of wildlife faeces ( $\mu_a=0$ ); (4) 150 contaminated patches (representing a  
15 dispersed defecation pattern) and almost complete avoidance of wildlife faeces (for 150  
16 contaminated patches  $\mu_a=0.75$ ). In order to include the effect of faecal decay, wildlife  
17 faecal decay rate was set so that at the end of the simulation (day 100), 10% of the initial  
18 wildlife faeces remained in the system ( $fa_{dk}=0.00001599$ ).

19

20 **Rotation grazing.** The same four scenarios described in the previous section were also  
21 used to investigate the interaction effects of defecation pattern and cattle level of  
22 avoidance of wildlife faeces within a rotational grazing scenario. For rotational grazing,  
23 the set stock pasture was divided into two pastures and three cattle were rotated round

1 each pasture twice. Only one of the pastures was simulated, thus the simulations were  
2 carried out on a 49 x 50 patch lattice. Each patch represented  $0.5\text{m}^2$  and the whole lattice  
3 represented a pasture of 0.125ha, half the size of the set stock pasture. The rotation was  
4 25 days in the simulated pasture, 25 days out, so that two complete rotations lasted 100  
5 days. To prevent ‘unrealistic’ overgrazing on the first day back in the pasture, the cattle’s  
6 daily intake requirement was set to the equivalent daily intake of cattle in a set stock  
7 environment ( $dR_k = 9000$ ).

8

### 9 **Measurements of forage availability**

10 | For the realistic grazing scenarios, i.e. the set stock and rotation grazing, measurements of  
11 | grass availability were gathered to ensure the model successfully created a heterogeneous  
12 | gap and tussock mosaic, and thus presented the grazing cattle with the nutrition versus  
13 | parasitism trade-off. The following statistics for grass availability were gathered over the  
14 | 10 repeated stochastic simulations:

- 15 | 1. The mean forage availability (number of bites available per  $0.5\text{m}^2$ ) of wildlife  
16 | faecal-contaminated patches with high cattle avoidance. No measurements of  
17 | forage availability were gathered for wildlife faecal-contaminated patches with no  
18 | cattle avoidance as tussocks would not form at these patches due to the non-  
19 | avoidance of the faeces.
- 20 | 2. The mean forage availability (number of bites available per  $0.5\text{m}^2$ ) of cattle  
21 | faecal-contaminated patches
- 22 | 3. The mean forage availability (number of bites available per  $0.5\text{m}^2$ ) of non-faecal-  
23 | contaminated patches.



1

## 2 **Measurements of cattle grazing behaviour**

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

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

10

## 11 **RESULTS**

12

13 **Forage availability in the set stock and rotation grazing systems.** Overall the mean  
14 number of bites of forage available in a 0.5m<sup>2</sup> patch of wildlife faecal-contaminated  
15 patches and cattle faecal-contaminated patches was greater than the mean number of bites  
16 of forage available in a 0.5m<sup>2</sup> patch of clean non-contaminated patches in both set stock  
17 and rotational grazing systems (Fig. 2). In the set stock system, at the maximum  
18 difference in forage availability, wildlife faecal-contaminated patches and cattle faecal-  
19 contaminated patches had 2.6 times and 2 times greater forage availability than the non-  
20 contaminated patches, respectively (Fig 2A). Similarly, in the rotational grazing system,  
21 at the maximum difference in forage availability, wildlife faecal-contaminated patches  
22 and cattle faecal-contaminated patches had 3 times and 2.3 times greater forage  
23 availability than the non-contaminated patches, respectively (Fig. 2B).

1

2 **Cattle avoidance of wildlife faeces.** Increasing cattle avoidance of wildlife faeces is  
3 associated with a decrease in the number of cattle bites from wildlife faecal-contaminated  
4 patches both pre- (days 1-30) and post-system equilibrium (days 31-100). However, post-  
5 equilibrium there is no difference in grazing contact levels between the three lowest  
6 avoidance levels ( $\mu_a = 0, 0.15$  and  $0.3$ ) (Fig. 3A). Increasing cattle avoidance of wildlife  
7 faeces is associated with an increase in the number of investigations of wildlife faecal-  
8 contaminated patches both pre- and post-equilibrium (Fig. 3B). The overall number of  
9 bites and number of investigations from cattle faecal-contaminated patches is  
10 significantly greater than the number of bites/investigations from wildlife faecal-  
11 contaminated patches (i.e. up to 46 times more bites and up to 14 times more  
12 investigations) (Figs. 3A & 3B).

13

14 **Defecation pattern.** Increasing the number of faecal-contaminated patches (i.e. more  
15 dispersed faecal-contamination patterns) is associated with an increasing number of cattle  
16 bites and investigations from wildlife-contaminated patches both pre- (days 1-50) and  
17 post-equilibrium (days 41-100) (Figs. 4A & 4B). However, the relative numbers of both  
18 grazing contacts and investigative contacts are less than commensurate with area. For  
19 example, defecation patterns with 150 contaminated patches lead to approximately only  
20 90 times greater number of bites compared to single patches. Additionally, defecation  
21 patterns with 150 contaminated patches lead to approximately 100 times greater number  
22 of investigations of wildlife-contaminated patches. The overall number of bites and  
23 number of investigations from cattle-contaminated patches is significantly greater than

1 the number of bites/investigations from wildlife faecal-contaminated patches (i.e. up to  
2 4251 times more bites and up to 191 times more investigations) (Figs. 4A & 4B).  
3  
4 **Set stock grazing.** The combined effects of avoidance and defecation pattern are  
5 consistent with the effects in isolation as modelled in previous simulations (Figs. 5A &  
6 5B). Thus, increased cattle avoidance of wildlife faeces results in reduced grazing  
7 contacts and increased investigative contact with wildlife faecal-contaminated vegetation.  
8 Defecation patterns with a greater number of contaminated patches result in increases in  
9 both grazing and investigative contacts. When comparing the magnitude of effects, level  
10 of faecal avoidance has a lesser effect than defecation pattern on the number of cattle  
11 contacts with faeces, e.g. dispersed patterns of both avoidance levels have a significantly  
12 greater number of grazing contacts and investigative contacts relative to single latrine  
13 patches (Figs. 5A & 5B). However, this observed increase in contacts with the number of  
14 contaminated patches is not commensurate with the area contaminated, e.g. 150  
15 contaminated patches result in only 105 times more bites than 1 contaminated patch.  
16 (Table.1). Pre-equilibrium (days 1-39), grazing contacts with wildlife faeces are greatest  
17 in scenario 3 (dispersed wildlife faeces and no cattle avoidance). In contrast, grazing  
18 contacts are greatest post-equilibrium (days 40-100) in scenario 4 (dispersed wildlife  
19 faeces and high cattle avoidance; Fig. 5A). Investigative contacts with wildlife faeces are  
20 highest in scenario 4 throughout the simulation (Fig. 5B). The overall number of bites  
21 and number of investigations from cattle faecal-contaminated patches are significantly  
22 greater than the number of bites/investigations from wildlife faecal-contaminated patches  
23 (up to 379 times more bites and up to 1463 times more investigations; Figs. 5A & 5B).

1

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

1 avoidance, and a dispersed defecation pattern with high cattle avoidance. There is also a  
2 greater number of investigations of wildlife faeces in a dispersed wildlife defecation  
3 pattern with high cattle avoidance relative to the number of bites and investigations from  
4 patches contaminated with cattle faeces (Figs 6A & 6B).

5

## 6 **DISCUSSION**

7

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

23

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

1

2 The varying defecation pattern scenarios demonstrated that dispersed defecation patterns  
3 result in a greater amount of grazing contacts and investigative contacts than latrines.

4 The grazing contact simulated here is consistent with the grazing study by Smith et al  
5 (unpublished), in which cattle grazed badger faecal-contaminated patches in a more  
6 dispersed faecal pattern faster than those concentrated in a single patch (i.e.  
7 representative of latrines). Thus the model has simulated successfully the patterns of  
8 grazing contact by cattle shown towards different types of faeces and different faecal  
9 defecation patterns.

10

11 In the more realistic set stock grazing scenarios (the interaction of avoidance and  
12 defecation pattern with faecal decay), the effects of avoidance and defecation pattern are  
13 similar to the effects of these factors in isolation. However, defecation pattern has a  
14 much stronger effect on disease risk than the level of cattle avoidance, with dispersed  
15 defecation patterns representing a significantly greater disease risk in terms of absolute  
16 grazing and investigative contact, relative to latrine-type defecation patterns. The risk of  
17 disease via grazing contact is also affected by the phase of the grazing process. In the  
18 early phase of set stocked grazing (pre-equilibrium), cattle have the greatest grazing  
19 contact with wildlife faeces where these faeces are dispersed and there is no cattle  
20 avoidance of them. The scenario of dispersed wildlife faeces and no cattle avoidance is  
21 representative of rabbit faeces and badger urinations, as cattle show no avoidance of  
22 either [6, 16] and they can both occur dispersed throughout the pasture [17, 34].

23 Microparasite numbers (e.g. *Mycobacterium*) are at their maximum and pose the greatest

1 disease risk when faeces are first deposited in the environment [33]. Rabbit faeces pose a  
2 risk of paratuberculosis (*Mycobacterium avium* subsp *paratuberculosis*) containing up to  
3  $4 \times 10^6$  colony forming units/g faeces [35]. Badger urinations pose a major risk of bovine  
4 tuberculosis (*Mycobacterium bovis*) containing up to  $3 \times 10^5$  colony forming units per ml  
5 of urine [36]. There will therefore be an enhanced risk of transmission of these diseases  
6 via the faecal-oral routes when cattle are first placed on a pasture.

7  
8 The patterns of contact observed in set stock grazing are similar to those in the rotational  
9 grazing scenario. Thus, during the first rotation of the rotation grazing scenarios, when  
10 cattle are first placed in the pasture, cattle have the greatest number of grazing contacts  
11 when wildlife faeces are dispersed and there is no cattle avoidance (i.e. representative of  
12 rabbit faeces and badger urinations). However, under rotation grazing, this risk is also  
13 amplified relative to the risk in a set stock environment. The greater levels of contacts in  
14 rotation grazing are largely driven by the increased stocking density in this grazing  
15 system. Whilst grazing, livestock selectively graze non-contaminated pasture and further  
16 contaminate clean areas with their own faeces. Thus, in rotational grazing the cattle are  
17 forced to graze fresh faeces faster and therefore increase their exposure to microparasite  
18 diseases such as paratuberculosis and bovine tuberculosis.

19  
20 In all of the grazing scenarios here, cattle have a greater overall number of grazing  
21 contacts and investigative contacts with their own faeces relative to the contacts with the  
22 wildlife faeces in the system. The simulations indicate that a major factor that drives  
23 cattle contact with faeces in grazing systems is the area of pasture that is contaminated.



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

16

17 Contact with a pathogen in the environment and the risk of disease from that pathogen is  
18 further complicated by the dose required for an effective transmission event e.g.  
19 infection. Dose-response assessment typically predicts that the probability of infection  
20 increases with increasing dose of a pathogen, in the shape of a sigmoid curve. In the  
21 simulations here, each contaminated patch in the dispersed faecal patterns contains fewer  
22 units of faeces, and therefore may have a lower dose of pathogen per patch. In contrast,  
23 at latrine sites, it is likely that there will be a far higher dose of pathogens present in the

1 patch. Currently, there are no definitive data to describe the relationship between  
2 exposure to pathogens in the environment and infection via the faecal-oral route.  
3 However, the disease risk associated with different faecal patterns will be dependent on  
4 the dose of the pathogen at a single patch, and the corresponding probability of infection  
5 on the dose-response sigmoid curve. If the dose of pathogen present in one dispersed  
6 faecal patch falls before the plateau of the sigmoid curve, the corresponding probability  
7 of infection for one contact with a dispersed patch will be less than the probability of  
8 infection for one contact with a latrine patch, which will have a greater dose of pathogen.

9 | In a number of the grazing scenarios simulated here (e.g. the set stock grazing), the  
10 | overall increase in grazing contact with dispersed faecal patterns relative to the grazing  
11 | contacts to latrine faecal patterns is a less than commensurate to the area of pasture  
12 | contaminated. Thus in these situations, latrine-type defecation patterns may pose a  
13 | greater risk of disease compared to dispersed faecal patterns. In contrast, in the rotation  
14 | grazing scenarios, the overall increase in grazing contact with dispersed faecal patterns  
15 | relative to the grazing contact with the latrine faecal patterns is commensurate with the  
16 | area of pasture contaminated, indicating that absolute contacts may provide a better  
17 | indication of disease exposure. If the dose from one dispersed faecal patch falls after the  
18 | plateau of the dose-response sigmoid curve then the corresponding probability of  
19 | infection for one contact with a dispersed patch will be equal to the probability of  
20 | infection for one contact with a latrine patch. Thus, the absolute contacts will determine  
21 | risk of disease and a dispersed defecation pattern will pose a greater risk of disease  
22 | relative to the latrine faecal patterns. The number of contacts relative to the area  
23 | contaminated is also affected by the grazing phase. In the pre-equilibrium phase of set

1 | stock grazing, there is a greater than commensurate increase in both grazing and  
2 | investigative contacts for dispersed faecal patterns with high cattle avoidance, relative to  
3 | the area of pasture contaminated. This is of applied significance for the management and  
4 | prevention of wildlife disease. For example, when cattle are first placed on a pasture in  
5 | areas with bovine tuberculosis in badgers, there may be a greater risk of infection from  
6 | faeces in areas of lower badger density (where faeces may be more dispersed) than in  
7 | areas of high badger density (where faeces are concentrated at latrine sites). Similarly,  
8 | the risk of infection may be increased by disturbance of the badger population during  
9 | culling operations, resulting in a more dispersed pattern of defecation.

10

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

1 quantify the risk of infection associated with these behavioural contact patterns for  
2 specific disease scenarios.

3

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8

#### 9 **DECLARATION OF INTEREST**

10 None

11

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- 23



1 Table 1: A comparison of the number of bites/number of investigation from dispersed  
 2 wildlife faeces (150 patches) relative to the number of bites/investigations from latrine  
 3 wildlife faeces (1 patch), for both levels of cattle avoidance in the set stock scenario and  
 4 the rotation grazing scenario.  
 5

	Relative No. of bites		Relative No. of investigations	
	No avoidance	High avoidance	No avoidance	High avoidance
<b>Set stock grazing</b>				
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
<b>Rotation grazing</b>				
Day 1-100				
whole simulation	140.35	151.50	173.45	150.91
Day 1-25				
1 <sup>st</sup> Rotation	139.88	167.42	188.27	161.65
Day 51-75				
2 <sup>nd</sup> Rotation	140.83	147.97	161.45	132.63

## 1 **Legends for Illustrations**

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

7

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

16

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

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

6

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

18

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

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

7

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

18

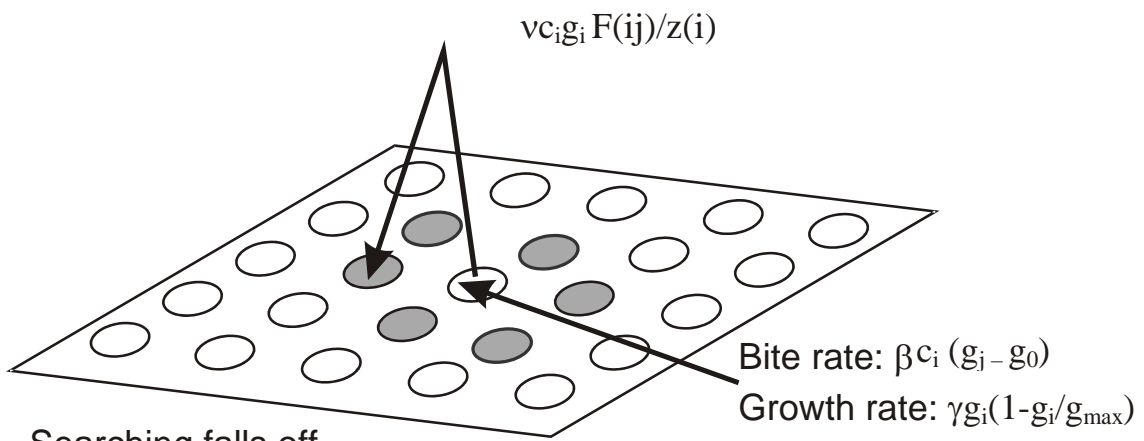
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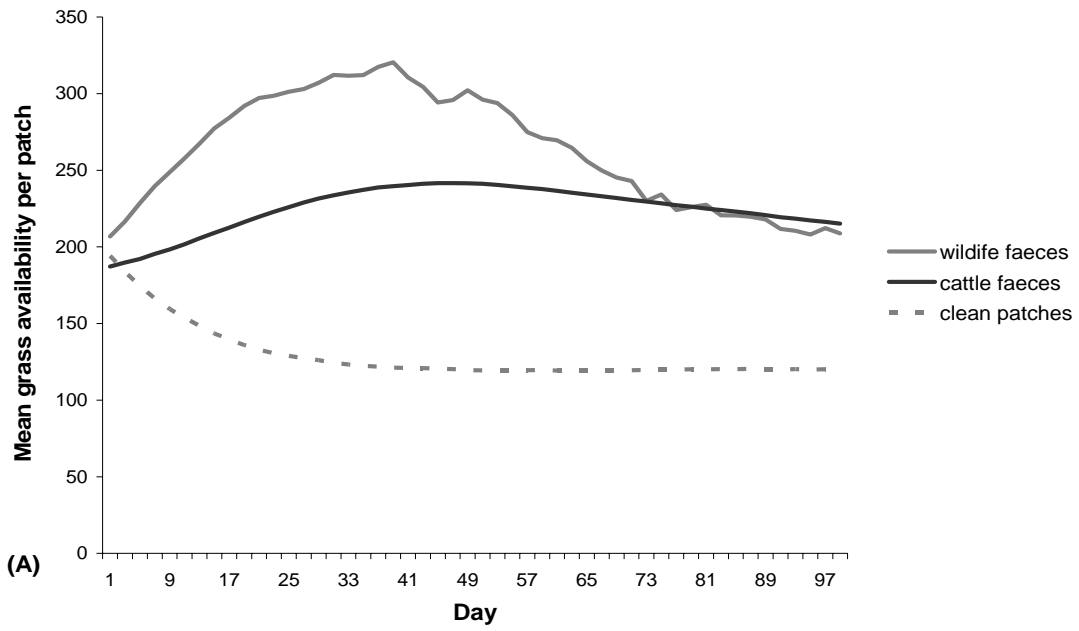
Searching falls off  
with distance:

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

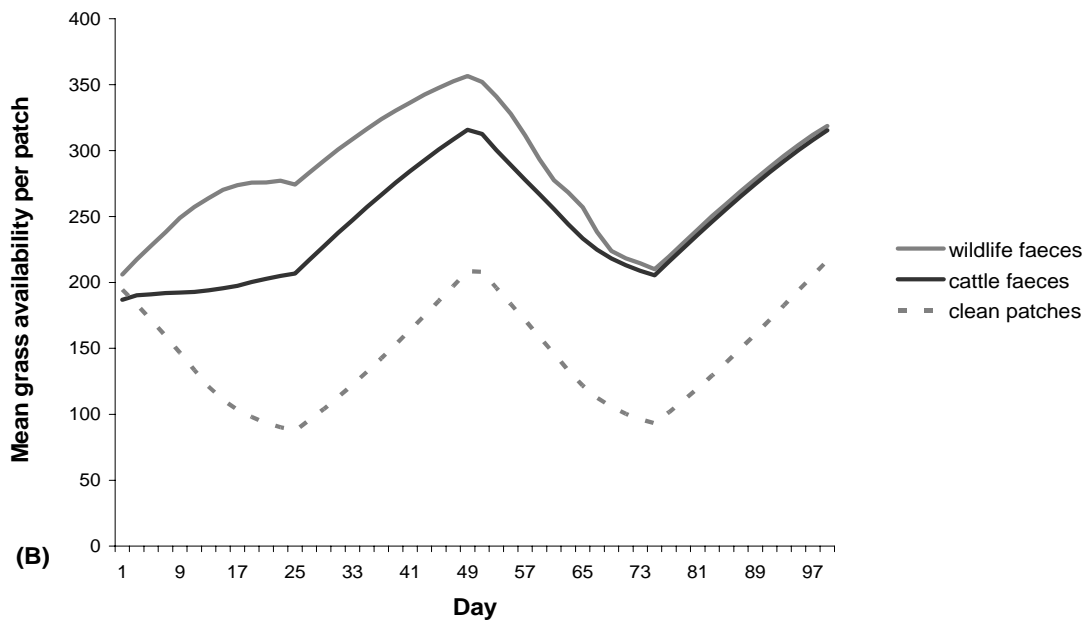
1

2

3 Figure 1

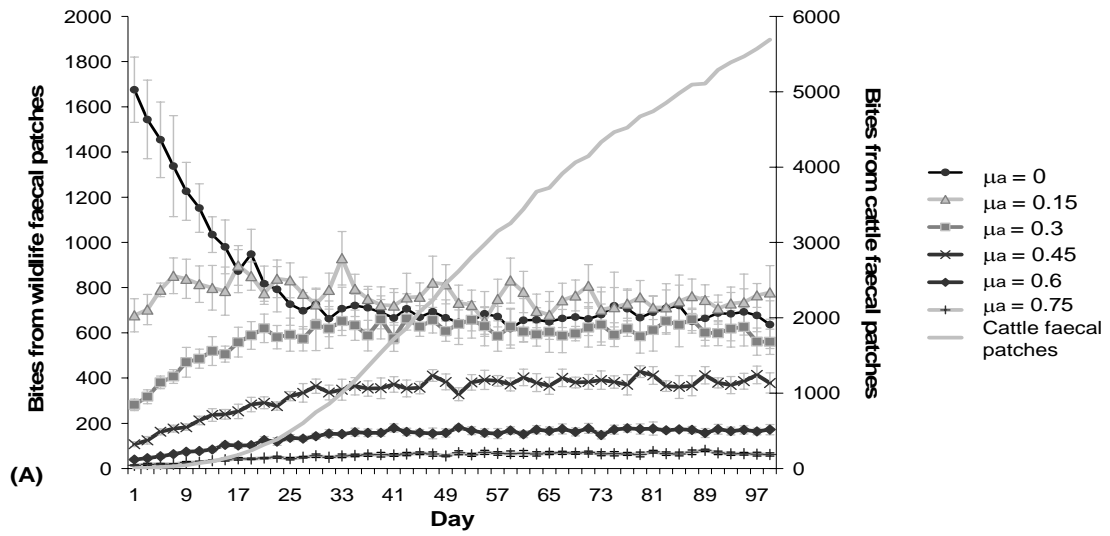


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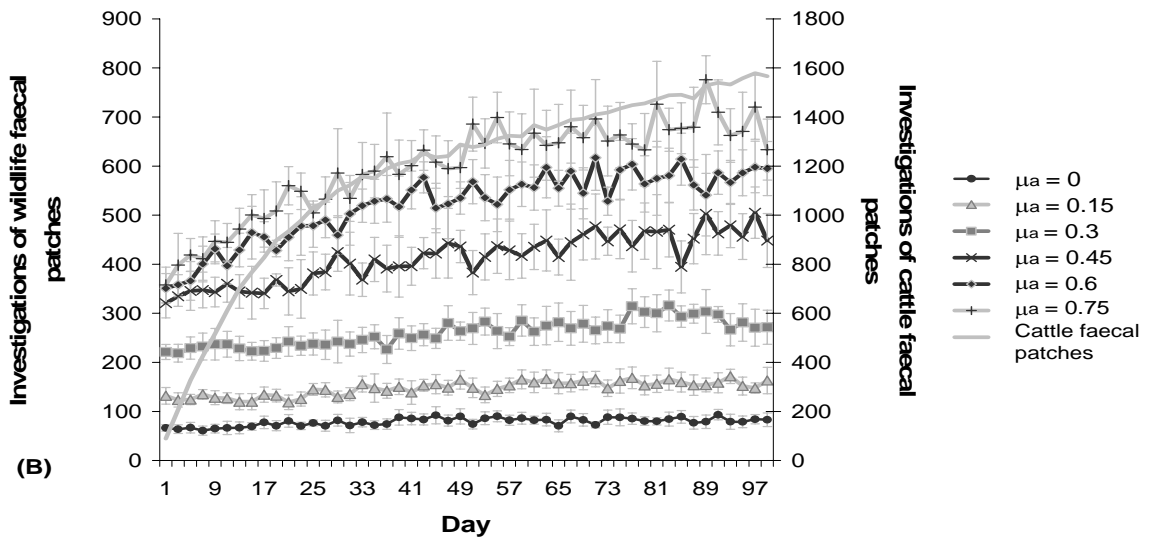


2

3 Figure 2

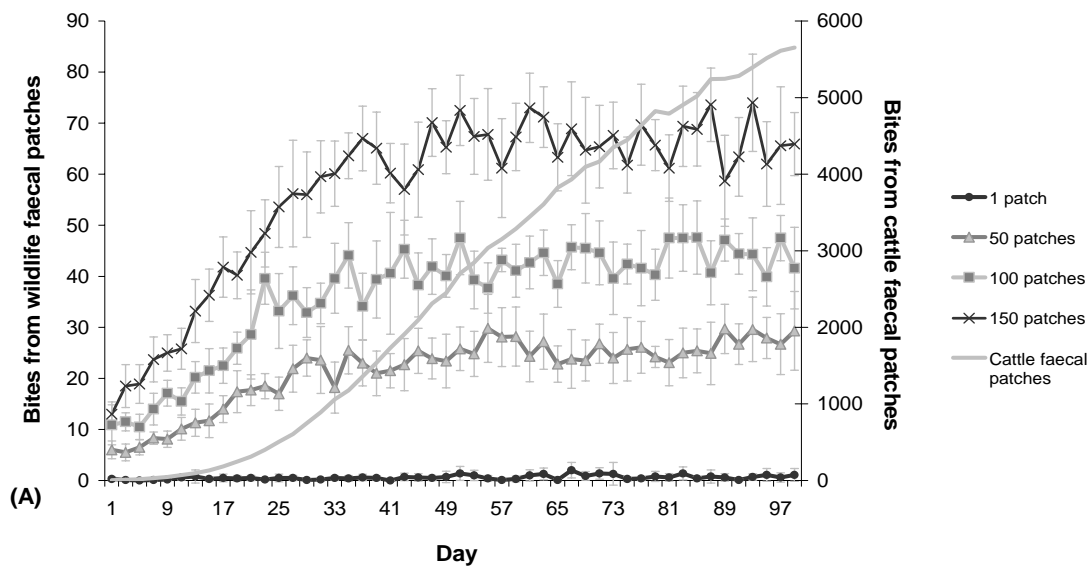


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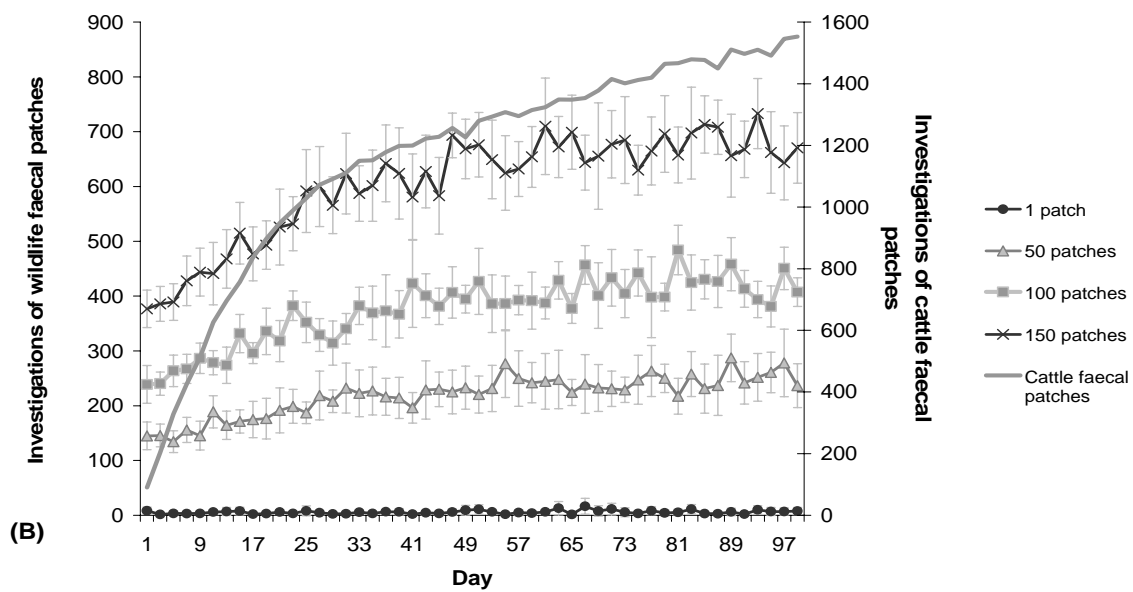


2

3 Figure 3



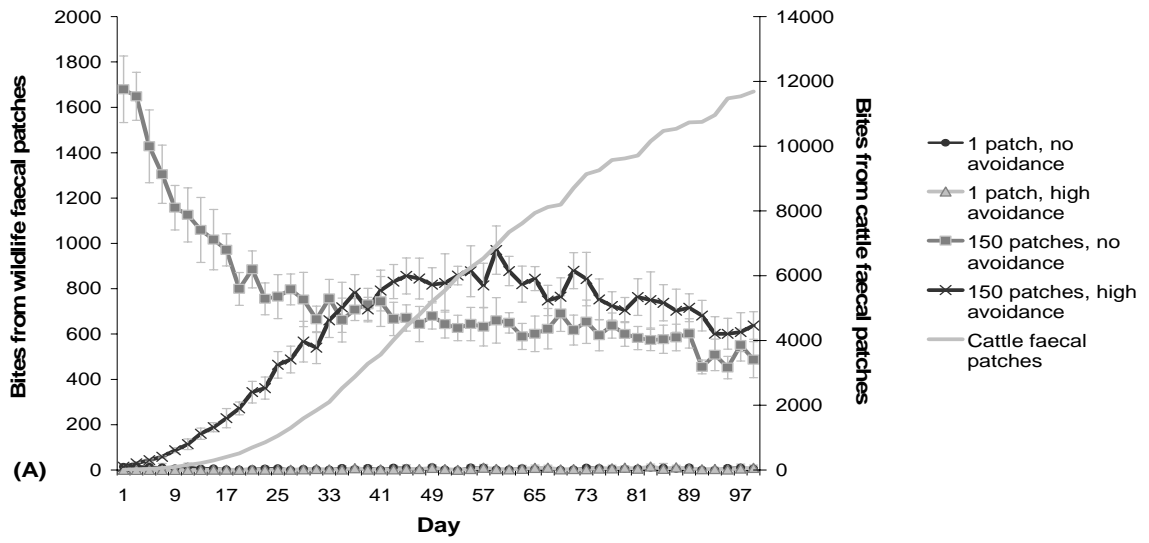
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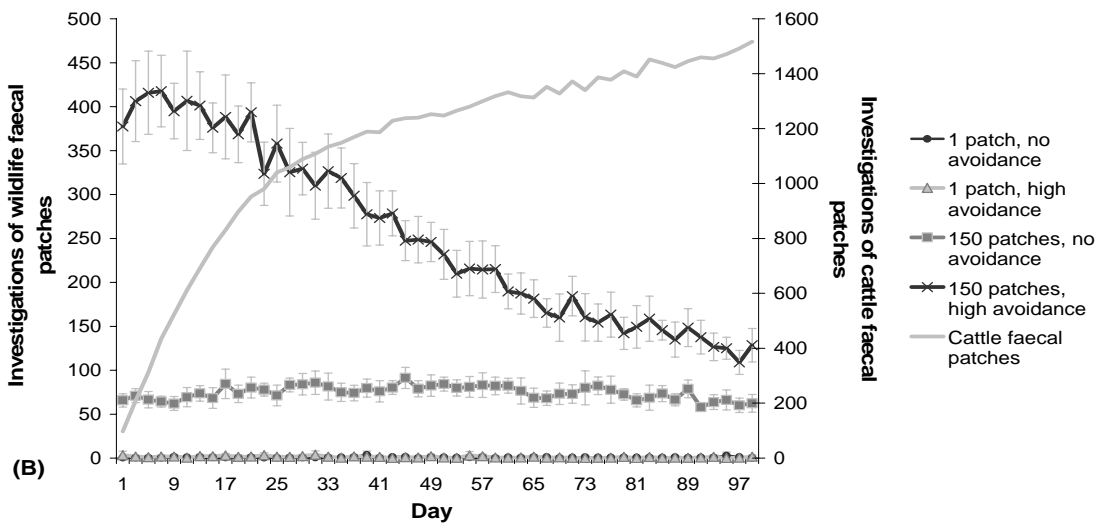
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3 Figure. 4



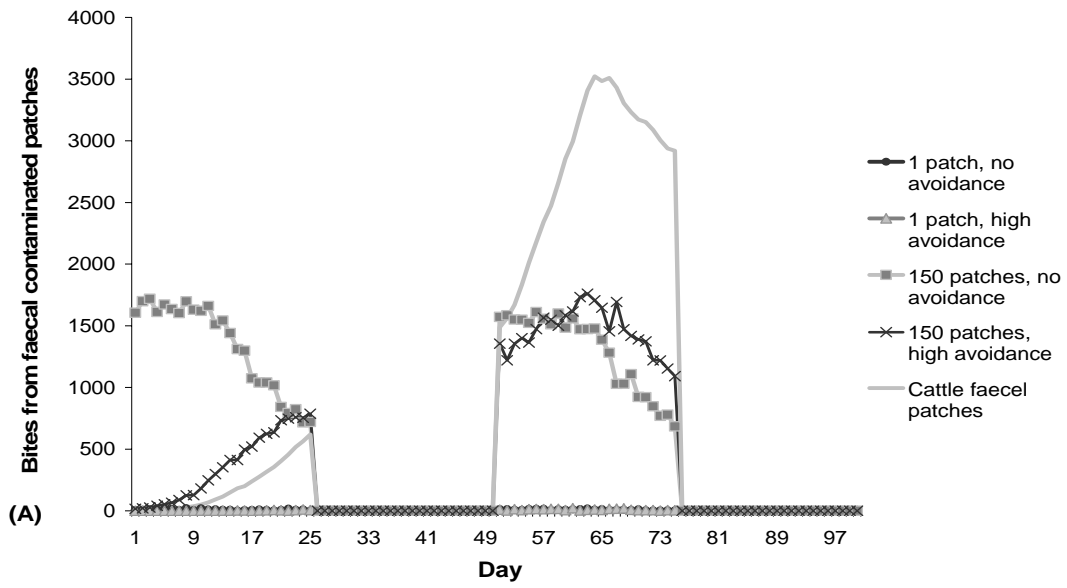


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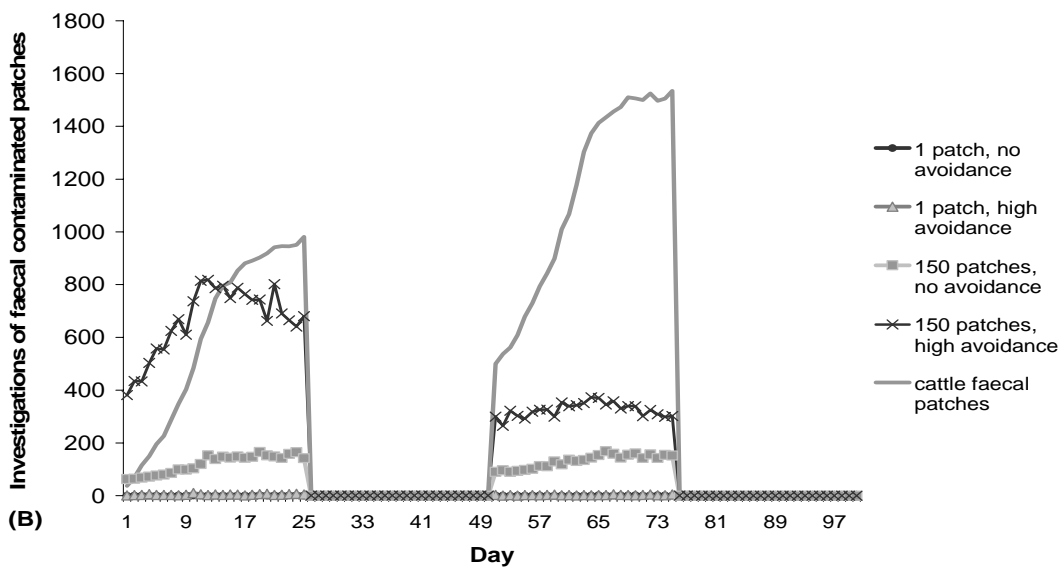


2

3 Figure 5



1



2

3 Figure 6

4