Livestock grazing behaviour and inter- vs intra-specific disease risk via the faecal oral route.

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Abstract

Livestock herbivores are at risk of inter- and intra-specific disease transmission via the faecal-oral route during grazing. The risk of disease from different host species will be dependent on the behavioural contact processes between the host herbivore and faeces in the environment at the bite scale. Here we use two grazing experiments to determine cattle's grazing response to both different types of host animal faeces and different defecation patterns, to establish their implications for disease transmission to grazing livestock. In experiment 1 there were five patch treatments of different faecal contamination (badger faeces, cattle faeces, deer faeces, rabbit faeces and non-contaminated control patches). In experiment 2 there were three treatment patterns of badger faecal contamination (one $1m^2$ circular patch contaminated with 960g of badger; two $1m^2$ circular patches each contaminated with 480g of badger faeces; and four $1m^2$ circular patches each contaminated with 240g of badger faeces). Sward selection was determined by measuring sward depletion at each of the treatment patches. In experiment 1 cattle grazed control and rabbit faecal contaminated patches the greatest, while badger contaminated patches were grazed the least. In experiment 2 cattle grazed the faecal pattern with the greatest number of contaminated patches the most suggesting that dispersed faecal patterns pose a greater disease risk that latrine sites. Given the

relatively more dispersed nature of rabbit faeces we conclude that rabbits represent a greater risk of paratuberculosis to cattle relative to the risk of tuberculosis from badgers.

Key words: disease transmission, faecal-oral route, livestock, wildlife host species, defecation pattern.

Introduction

Both macroparasites (e.g. parasitic helminths) and microparasites (e.g. bacterial pathogens) are found in the faeces of host animals and can be transmitted via the faecal-oral route whilst grazing (Sykes, 1987). However, herbivores generally avoid grazing near swards contaminated with faeces (Bao et al, 1998; Forbes and Hodgson 1985; Hutchings *et al*, 1998). This instinctive behaviour is believed to have evolved as a method of parasite avoidance (Hart 1990; Lozano, 1991) and has been shown to significantly reduce herbivores intake of parasite larvae (Michel, 1955; Carbaret et al, 1986). Faeces-avoidance grazing behaviour creates a heterogeneous landscape of gaps (short, non-contaminated, grazed patches) and tussocks (tall, faeces-contaminated, avoided patches) (Hutchings *et al*., 2001a). Furthermore, nutrient leaching from faecal deposits may result in the faecal-contaminated tussocks of grass having relatively high nutrient contents (Haynes & Williams, 1993). Grazing herbivores use cues of both sward height and sward tone in order to preferentially select swards with the greatest forage intake and greatest nutrient content (Bazely, 1990). Thus the gap and tussock mosaic presents the herbivore with a nutrition vs parasitism trade-off in that the faeces-contaminated tussocks are localised concentrations of both nutritional resources and parasites (Hutchings *et al*., 2000, 2001a). Herbivores must make grazing decisions in this heterogeneous environment which will determine their intake of nutrients and parasites and in turn their fitness and survival. Transmission of parasites to grazing herbivores will be dependent on the behavioural contact processes between the host herbivore and faeces in the environment at the bite scale.

Grazing herbivores share their environment with a number of other host animal species, and as such the grazing environment will be contaminated with their own faeces and faeces of other species. The faeces from different species pose a risk of a number of different diseases to grazing livestock. Cattle are at risk of bovine tuberculosis from badger faeces (Muirhead et al, 1974) and paratuberculosis from rabbit faeces (Beard et al, 2001; Daniels et al., 2001). Whilst deer have been implicated in the transmission of both bovine tuberculosis (Gunning, 1985; Dalahay *et al*, 2007) and paratuberculosis (Chiodoni & Vankruiningen, 1983) to grazing livestock. Thus, there is the potential for indirect inter-specific disease transmission via the faecal-oral route during grazing. Studies investigating the herbivores grazing response to faeces of a single host species, suggest that herbivores may vary their level of avoidance of faeces, e.g. cattle show a strong avoidance of both badger faeces (Hutchings and Harris, 1997; Hutchings and Harris, 1999) and their own faeces (Forbes and Hodgson, 1985) and no avoidance of rabbit faeces (Daniels et al., 2001; Judge et al, 2005). However, there are no studies investigating the herbivores grazing response to the faeces of different host species relative to each other in the one grazing system. Livestock herbivores avoidance of host animal's faeces will affect their amount and type (grazing and investigation) of contact with faeces and thus parasites in the environment. As such, data on the herbivores avoidance of different host animal faeces relative to each other in the one grazing system will provide information on the relative risk associated with different diseases from host animal species.

However the faeces of different host species also varies in defecation pattern. Animal defecation patterns differ both between species and within species, from single deposits dispersed throughout the environment, to the accumulation of faeces at latrines. For example, rabbits deposit faecal pellets both randomly within their home range and at latrine sites (Sneddon, 19991). Badgers tend to accumulate defecations at latrines, however at lower densities there is an increasing number of single defecations throughout their habitat (Hutchings et al., 2001b). The herbivores strength of avoidance of faeces increases with the amount of faeces present in a patch (Hutchings et al., 1998) thus defecation pattern may affect herbivore contacts (ingestion and investigation events) with faeces. These faecal patterns represent patterns of pathogen distribution, and thus each contact (e.g. bite) represents a potential disease contact event, and thus risk of disease transmission.

Thus, herbivore contact with disease in the grazing system is driven by a number of factors creating a complex interplay between herbivore behaviour and the environment. This paper aims to isolate and quantify the individual effects of faeces from different host animal species and deposition pattern, then determine their implications for the risk of disease transmission to livestock. Here we report on two grazing experiments. Experiment 1, set out to determine the grazing response of cattle to faeces of different species and the effect of the nutritional environment on this grazing response. Experiment 1 tests the null hypothesis that there will be no difference in contact behaviour of cattle with faeces from different species. Experiment 2, set out to determine the effect of different spatial patterns of faeces in the environment on cattle contact with faeces, and thus risk of disease transmission. Experiment 2 tests the null hypothesis that there will be no difference in contact behaviour of cattle with faeces in different defecation patterns.

Material and methods

Experimental design

Experiment 1. The experiment was conducted in spring 2005 on a 2-ha experimental field plot, which was divided into four 0.5-ha plots. There were two environment treatments and five patch treatments of different faecal contamination. The environment treatments consisted of a high nitrogen (high-N) treatment and a low-nitrogen (low-N) treatment. To create the treatments, prior to the start of the experiment, half the plots were fertilised (Nitraprill at a rate of 65 kg N/ha and 32.5 kg P/ha), and half the plots were left unfertilised (no fertiliser for 12 months). There were two plots per treatment. The five patch treatments consisted of four types of faecal contamination (120g badger faeces, 120g cattle faeces, 120g deer faeces, 120g rabbit faeces) and a non-contaminated control treatment. In each plot there were 20 patches (4 rows of 5 patches), of $0.5m^2$ in size and each patch treatment was randomly allocated within each row. Prior to the start of the experiment the patches were covered with exclusion cages and the plots were grazed by a pool of 16 1yr old Aberdeen Angus bullocks, managed to create a gap and tussock mosaic according to Hutchings et al (2002). Thus, each experimental patch had increased sward surface height (SSH) compared to the surrounding plot areas. Once, there was a visible difference in sward height between the patches and the surrounding area (see environmental measurements below), the experiment commenced and was run over a period of 12 days. Four cattle were placed in each plot, and in order to minimise any effects of plot differences on diet selection, each group of cattle was rotated round the plots on a daily basis. Thus each group experienced each plot three times over the course of the experiment.

Experiment 2. The experiment was conducted in spring 2006 on a 3-ha experimental field plot, which was divided in six 0.5-ha plots. There were three faecal pattern treatments. Faecal pattern 1 consisted of one $1m^2$ circular patch contaminated with 960g of badger; faecal pattern 2 consisted of two $1m^2$ circular patches each contaminated with 480g of badger faeces, and faecal pattern 3 consisted of four $1m^2$ circular patches each contaminated with 240g of badger faeces. A treatment patch area of $1m^2$ was chosen as it represents the approximate active area of a badger latrine (Brown, 1993). The minimum contamination level of 240g of badger faeces per $1m^2$ was selected as this is the same amount of faeces per unit area used in experiments 1. All patches were randomly placed within their plots. Thus each treatment had the same overall amount of badger contamination in each plot (960g) with varying defecation patterns and varying concentrations of faeces in each patch. Each treatment was randomly allocated to a plot so there were 2 field plots of each faecal pattern treatment. Prior to the start of the experiment the plots were left ungrazed to ensure both patches and the surrounding areas in each plot had a uniform sward surface height. The experiment took place over a period of 12 days. Four cows with their calves were placed in each plot, and in order to minimise any effects of plot differences on diet selection, each group of cattle was rotated round the plots on a daily basis. Thus each group experienced each plot twice over the course of the experiment.

Animals

Experiment 1. Sixteen 1yr old Aberdeen Angus bullocks were selected randomly from a commercial herd and divided into four groups balanced for live weight (live mean weight 441.6 ± 4.8kg [mean ± SE]). All animals were treated with a broad spectrum anthelmintic (Invermecton) prior to the start of the experiment to remove any parasitism. Faecal egg counts (number of parasite eggs excreted per gram of cattle faeces) confirmed that all animals possessed negligible parasite burdens

Experiment 2. Twenty-four Angus-Limouson cross cows, each with a single calve at foot (calves were 8-9 weeks old and carried out limited grazing on the pasture), were selected from a commercial herd and divided into six groups balanced for live weight (live mean weight 599.1 ± 10.2kg). All animals were treated with a broad spectrum anthelmintic (Invermecton) prior to the start of the experiment to reduce any parasitism. Faecal egg counts (number of parasite eggs excreted per gram of cattle faeces) confirmed that all animals possessed negligible parasite burdens.

Environmental measurements

Experiment 1. Stratified SSH measurements of background sward structure were measured on day 0 (pre experiment), day 7 (mid exp) and day 12 (end exp), using a sward stick, in both faeces contaminated tussocks and non-contaminated gap swards walking along a W-transect of the plot. On the same sampling days composite mean sward samples of gap areas and tussock areas in each plot were collected for chemical analysis. For the experimental treatment patches, on day 0 SSH of patches was measured using a sward stick taking three sward heights from each treatment patch. In order to ensure minimal effect on the vegetation in the patches at day 0, composite mean sward samples were collected from all the patches in the N+ treatment and all the patches in the N- treatment for chemical analysis. On day 12 each $0.5m^2$ patch was sampled individually by cutting the sward to the soil surface.

Experiment 2. SSH measurements of background sward structure were measured using a sward stick walking along a W-transect of the plot on a daily basis. Once a gap and tussock mosaic had formed (Day 8), sward height measurements were stratified, taking heights from both faecal contaminated tussocks and non-contaminated gap swards. On days 0 (pre exp), 7 (mid exp) and 12 (end exp) three composite mean sward samples were collected for chemical analysis from the non-patch areas in each of the plots. For the treatment patches, on day 0 SSH of patches was measured using a sward stick taking three sward heights from each treatment patch. In order to ensure minimal effect on the vegetation in the experimental treatment patches, composite mean sward samples were collected from all the treatment patches contaminated with badger faeces. On day 12 each $1m^2$ circular patch was sampled individually by cutting the sward to the soil surface.

Common protocol for experimental measurements

All sward samples were dried in a hot air oven to provide a dry matter (DM) estimate that was analysed for nitrogen content and % digestive organic matter in dry matter (DOMD) using near-infrared spectroscopy.

Animal grazing behaviour

Experiment 1. Grazing behaviour was recorded using measurements of sward surface height. Three heights were taken daily at each of the $0.5m^2$ contaminated patches using a sward stick. Thus, grass depletion/cattle grazing at each treatment patch was measured on a daily basis. Grazing behaviour was also measured by direct behavioural observations by one observer from 1 of 2 observation towers overlooking the experimental plots 5m above ground level. Observations were carried out on randomly selected individuals for 5-min period of activity. All individuals were recorded twice a day giving a total of 384 focal observations of 5min each over the 12-day period. The following grazing variables were recorded during each observation.

1. No of bites taken from each patch type. A bite was defined as a head pull with the severing of herbage.
2. No of investigations from each patch type. An investigation was defined as contact with the sward patch with no severing of herbage.
3. Bite rate (bites per second)

Experiment 2. Grazing behaviour was measured using measurements of sward surface height. Three heights were taken at each of the 1m^2 circular patches using a sward stick (Barthram, 1985). Thus, grass depletion/cattle grazing at each patch was measured on a daily basis. An active transponder system (Hutchings & Harris, 1996) was used to monitor the contact patterns of the animals with each patch, however due to repeated power failures disrupting the data collection, there was insufficient data collected for analysis.

Statistical analysis

Analysis of variance (ANOVA) was used to determine treatment effects on background sward characteristics (SSH, nitrogen content, % DOMD, DM content) at day 0 for both experiment 1 and 2, and treatment effects on the SSH of experimental patches at day 0 for experiment 1. For the background sward characteristics in Experiment 1 plot treatment (High N/Low N) and sward type (gap swards/tussock swards) were used as treatments. Plot was used as the block term for SSH, but no blocking structure was used for the other background sward characteristics. For the SSH at experimental treatment patches, plot treatment (High N/Low N) and patch treatment (type of faecal contamination) were used as treatments with patch nested in plot as the block term. In experiment 2 the effects of treatment pattern (faecal pattern 1 vs faecal pattern 2 vs faecal pattern 3) on the SSH of the experimental treatment patches at day 0 were analysed using residual maximum likelihood (REML; Patterson & Thompson, 1971). The model included treatment pattern as fixed effects and patch nested in plot as random effects.

The amount of grass grazed from each experimental treatment patch (both experiment 1 and 2) was determined by calculating the overall grass depletion per patch (mean SSH day 0 – mean SSH day 12) and the area under the curve (AUC) for SSH per patch per day (calculated by the trapezoidal method). Plot treatment and patch treatment effects on the grass depletion per patch and the AUC for SSH were determined in experiment 1 using ANOVA, with patch nested in plot as the block term. For experiment 2 patch treatment effects on the grass depletion per patch and the AUC for SSH were determined using REML, with patch nested in plot as random effects.

The behavioural observation data from experiment 1 was not normally distributed and thus patch treatment effects on the number of bites and the number of investigations from each patch treatment in each plot was analysed using Friedman's test. Spearman's ranked correlation coefficient was used to investigate the relationship between both the number of bites and the number of investigations from each patch with grass depletion from each patch. The effects of animal and plot on cattle bite rate were analysed REML. The model included animal number and plot number as fixed effects and cattle group as random effects.

Results

Environmental measurements

Experiment 1. On day 0 (pre experiment), tussock swards from the non-patch areas had a greater SSH (mean SSH tussock swards 14.97 ± 0.18cm [mean ± SE]; mean SSH gap swards 3.37 ± 0.18cm ($F_{1, 154}$ = 2107.34, $P < 0.001$)) and a greater nitrogen content (mean nitrogen content tussock swards 32.0 ± 2.39; mean nitrogen content gap swards 20.4 ± 2.39 ($F_{1,4}$ = 11.83, $P<0.05$)) compared to gap swards. However, there was no effect of plot treatment on SSH (mean SSH 9.17 ± 0.30cm ($F_{1, 154}$ = 1.67, P > 0.05)), nitrogen content (mean nitrogen content 26.2 ± 3.38 ($F_{1, 4}$ = 0.02, P > 0.05)), % DOMD (mean DOMD 79.62 ± 0.53 % ($F_{1, 4}$ = 0.11, P > 0.05)), or dry matter content (mean DM content 218.6 ± 11.32 g/kg fresh matter ($F_{1, 4}$ = 0.00. P > 0.05)) in the day 0 grass samples. Additionally for treatment patches there was no effect of plot treatment ($F_{1, 2}$ = 0.44, P > 0.05) or patch treatment ($F_{4, 68}$ = 0.90, P > 0.05) on day 0 patch sward height (mean SSH 13.77 ± 1.20cm). As the fertilizer regime failed to create environmental differences, data were pooled to investigate experimental patch treatment effects for cattle grazing behaviour.

Experiment 2. On day 0 (pre-experiment), there was no effect of faecal treatment pattern on nitrogen content (mean nitrogen content 27.48 ± 1.84 g/kg DM, $F_{2, 3}$ = 0.68, P > 0.05), % DOMD (mean DOMD 75.56 ± 0.30 %, $F_{2, 3}$ = 2.50, P > 0.05), or dry matter content (mean DM content 217.5 ± 10.62 g/kg fresh matter, $F_{2, 3}$ = 0.86, P > 0.05) between each plot. Day 0 swards heights showed no effect of treatment pattern on the non-patch SSH (mean SSH 19.62 ± 0.78cm, ($F_{2, 3}$ = 0.87, P > 0.05)) or contaminated patch sward surface height (SSH 17.67 ± 0.430cm, W_2 = 0.01, P > 0.05)). Thus, at the beginning of experiments there was no difference between plots and patches.

Cattle grazing behaviour and sward depletion

Experiment 1. Patch treatment had a significant effect on the AUC for SSH per patch over the course of the experiment ($F_{4, 68}$ = 28.04, P < 0.001). Badger contaminated patches had the greatest AUC, followed by cattle and deer. Rabbit and control patches had the lowest AUC (Fig. 1). Patch treatment also had a significant effect on sward depletion (mean SSH day 0 – mean SSH day 12) by cattle ($F_{4, 68}$ = 59.06, P < 0.001). Cattle grazed control and rabbit patches the most, followed by deer and cattle contaminated patches. Cattle grazed badger contaminated patches the least (Fig. 2). Patch treatment had a significant effect on the number of bites observed from each patch treatment in each plot (S_4=12.10, $P < 0.05$) (Table. 1), and a significant positive relationship between the number of bites from each patch and the sward depletion from each patch (r_s=0.362, $P < 0.001$). There was no effect of patch treatment on the number of investigations from each patch treatment in each plot (S_4 = 4.44, $P > 0.05$) (Table. 3), and no relationship between the number of investigations from each patch and the sward depletion. There was no difference in bite rate between animals (W_{15} = 1.21, $P > 0.05$) or plot (W_3 = 1.35, $P > 0.05$) (mean bite rate 0.99 ± 0.06 bites per second).

Experiment 2. Faecal treatment pattern had a significant effect on the AUC for SSH per area type over the course of the experiment (W_5 = 57.99, $P < 0.001$). However, there was no significant difference in the overall?? AUC between different faecal treatment patterns. The badger contaminated experimental patches had a significantly greater AUC compared to that of the background SSH. Additionally, there was a significant difference in the AUC of the background SSH between the different faecal treatment patterns, with treatment pattern 3 (four patches contaminated with 240g of badger faeces per plot) having a significantly greater AUC compared to treatment pattern 1 (one patch contaminated with 960g of badger faeces per plot) (Fig. 3). Treatment pattern has a significant effect on sward depletion at badger contaminated patches by cattle (W_2 = 16.6, $P < 0.001$). Cattle grazed contaminated patches under treatment pattern 3 (four patches contaminated with 240g of badger faeces) the most, followed by those in treatment pattern 2 (two patches contaminated with 480g of badger faeces), and those in treatment pattern 1 (one patch contaminated with 960g of badger faeces) the least (Fig. 4).

Discussion

The aim of this study was to determine the herbivore grazing response to faeces from different host animal species and deposition patterns. Cattle varied their avoidance of different types of faeces within the one grazing system, suggesting wildlife host species pose different disease risks to grazing herbivores. However, the temporal behavioural pattern of cattle to faecal contaminated vegetation is the same for cattle faeces, badger faeces and deer faeces i.e. there is a period of avoidance before cattle graze the faecal contaminated patch. In contrast, rabbit and control patches were grazed with no period of avoidance. The disease risk associated with a particular host animal faeces will also be dependent on the type of pathogen present in the faeces. Macroparasites take a number of weeks to develop into infective stage larvae and migrate from the faeces into the surrounding sward, where they represent a risk of infection (Familton and McAnulty, 1997). Thus, the delayed grazing contact observed in the badger, cattle and deer faeces suggests they pose an increased risk of macroparasite (e.g. gastrointestinal nematodes) transmission via ingestion of faecal contaminated vegetation. In contrast, microparasite numbers (e.g. *Mycobacterium*) are at their maximum and pose the greatest disease risk when faeces are first deposited in the environment (King et al, 1999). Thus, the results here suggest that for disease transmitted via ingestion of contaminated forage, low levels of cattle faecal avoidance, i.e. cattle none-avoidance of rabbit faeces, present the cattle with the a greater risk of microparasite disease transmission. Rabbits have been highlighted as a potential reservoir of paratuberculosis (Judge et al, 2006) and the results here indicate that rabbit faeces pose a high risk of disease to cattle via the faecal-oral route, relative to other types of faeces. In contrast, a high level of cattle avoidance i.e. cattle avoidance of cattle faeces, results in an initial reduction in grazing of contaminated patches, and therefore a reduction in the risk of intra-specific disease transmission. Cattle show a similar high avoidance of badger faeces, suggesting that rabbits pose a greater inter-specific disease risk to grazing cattle relative to badgers for micro-parasitic infections. Thus, all else being equal rabbits pose a far greater risk of paratuberculosis to cattle than the risk of tuberculosis from badgers.

The pattern of contamination in the grazing environment also affected cattle grazing behaviour, with cattle showing a greater level of avoidance of single patches of faeces with a greater amount on faeces. The results indicate that defecation patterns with an increasing number of contaminated patches, i.e. representative of more dispersed defecation patterns, will experience a greater number of grazing contacts. Use of latrines or selective elimination has been hypothesised to be a method of parasite avoidance, whereby animals selectively defecate in areas that are not used for foraging in order to reduce intra-specific exposure to parasites (Hart, 1990). The results presented here suggest that latrine defecation sites may also promote parasite avoidance between different host animal species. Thus, animals such as badgers which defecate at latrine sites (e.g. for scent marking) may act to reduce livestock exposure to their parasites and pathogens. In contrast, wildlife host animals which defecate randomly across the pasture may increase cattle contacts with faeces. Thus, all else being equal in terms of defecation pattern, rabbits represent a greater risk of paratuberculosis to grazing cattle relative to the risk of tuberculosis from badgers. However, badgers at lower densities who deposit a greater number of single defecations throughout their habitat may result in increased cattle contacts compared to faeces at latrine sites. These results support Hutchings *et al*. (2001b) who proposed that faecal patterns from low density badgers may increase cattle contact rates with badger faecal contaminated pasture and thus increase the risk of bovine tuberculosis to cattle. This is also consistent with the recent findings of perturbation effects of badger population reduction on tuberculosis risk to cattle i.e. the risk of tuberculosis to cattle can increase following badger culling (Donnelly et al, 2003; Woodroffe et al, 2006).

However, contact with a pathogen in the environment and the risk of disease from that pathogen is further complicated by the dose required for infection. Dose-response assessment predicts the probability of infection for a given amount of contamination increases with increasing dose of a pathogen, in the shape of a sigmoid curve (Clarkson, 1991). Each patch of vegetation contaminated from a host animal with a dispersed faecal pattern, will have less contamination relative to a clumped or latrine pattern. As such, contaminated patches from dispersed faecal patterns will represent a lower dose of pathogen per patch. Currently, there is no definitive data to describe the relationship between exposure to pathogens in the environment and subsequent infection via the faecal-oral route. However, the disease risk associated with different faecal patterns will be dependent on the dose of pathogen at a single patch, and the corresponding probability of infection on the dose-response sigmoid curve. If the dose of pathogen present in one dispersed faecal patch falls before the plateau of the sigmoid curve then the corresponding probability of infection for one contact with a dispersed patch will be less than the probability of infection for one contact with a latrine patch, which will have a greater dose of pathogen. It is therefore possible that despite cattle having less grazing contact with latrine type faecal patterns, the dose of pathogen in the contaminated patches may result in increased risk of disease from latrines relative to the risk from dispersed faecal patterns. In this case, the risk of tuberculosis from badgers may pose a greater risk to cattle than the risk of paratuberculosis from rabbit faeces. In contrast, if the dose from one dispersed faecal patch falls after the plateau of the dose-response sigmoid curve then the corresponding probability of infection for one contact with a dispersed patch will be equal to the probability of infection for one contact with a latrine patch. In this case, each contact can be considered a disease transmission, and dispersed faecal patterns which result in a greater number if grazing contacts, will pose a greater risk of disease relative to the latrine faecal patterns. Dose-response relationships will depend on environmental factors and the specific disease in question. However, for faecally mediated disease contact patterns with contaminated patches will underlie the disease dynamics. This highlights need to establish the relationship between exposure to a specific dose of pathogen in the environment and subsequent infection, in order to determine the risk of disease associated with the behavioural response of livestock to faeces in the environment.

This study has shown that both the type of faeces and pattern of faeces have an effect on cattle contact with faecal contaminated patches, and therefore the risk of inter- vs intra-specific disease via the faecal-oral route from different host animal species. The behaviour of livestock in complex grazing environments plays an important role in livestock exposure to parasites and highlights the significance of livestock behaviour as a driver of disease dynamics.

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Table 1. Effect of patch treatment (type of faecal contamination) on the cattle grazing behaviour of treatment patches. Values given are the median number of bites and number of investigations per patch treatment over the whole experiment (with minimum and maximum values).

Patch Treatment	Badger	Cattle	Deer	Rabbit	Non-contaminated Control	Patch Treatment Effects
Bites	0 (0-3)	12 (3-17)	29.5 (20-38)	24 (10-81)	28.5 (13-45)	*
Investigations	7.5 (6-8)	7.5 (4-15)	5 (4-7)	9.5 (7-14)	6 (5-9)	NS

NS = P>0.05, *P<0.05.

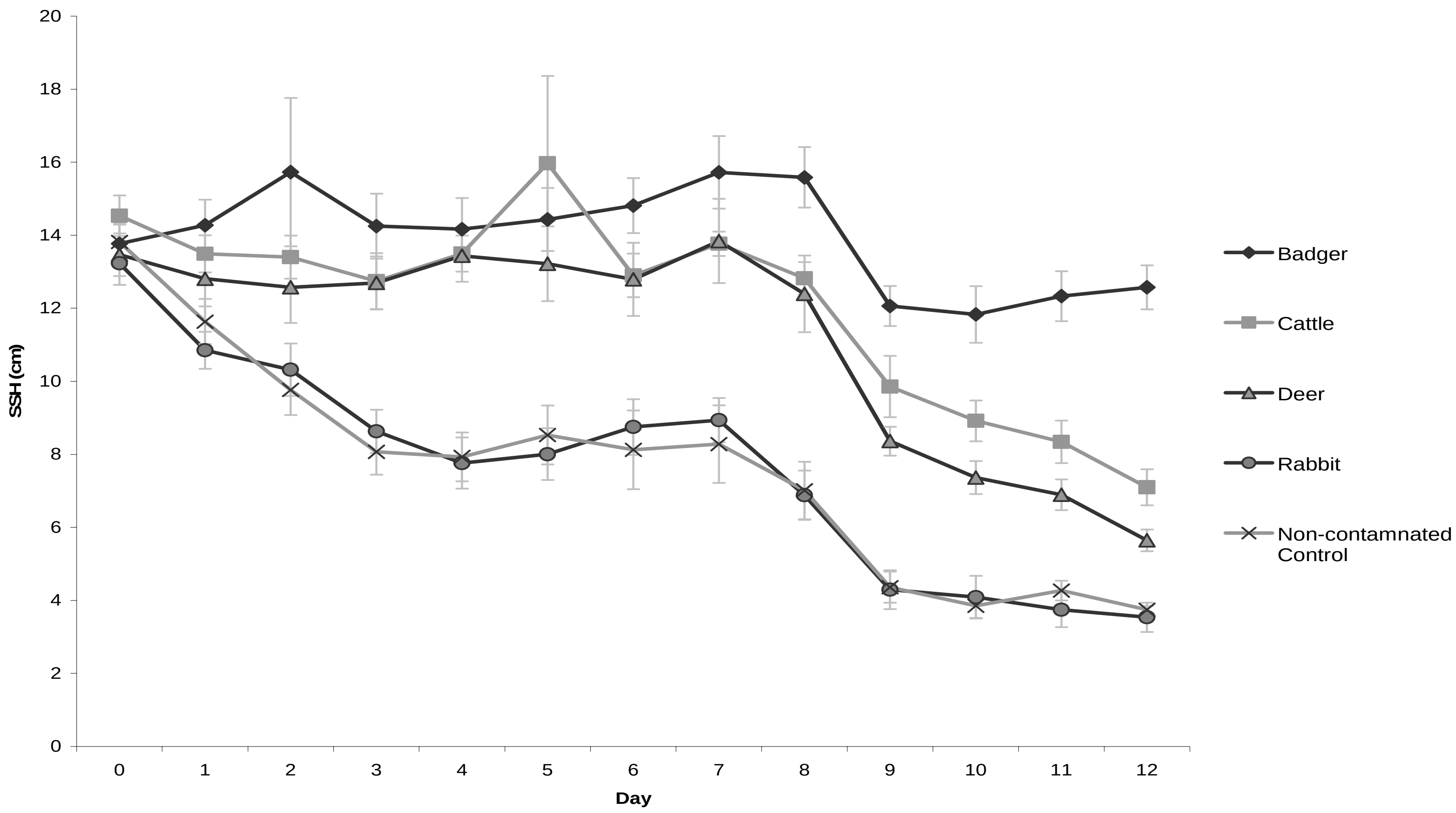

Fig.1: Effect of patch treatment (type of faecal contamination) in the type of faeces trial, on sward surface height (SSH). Figures are the mean sward surface height (SSH) per patch treatment, per day ±SE.

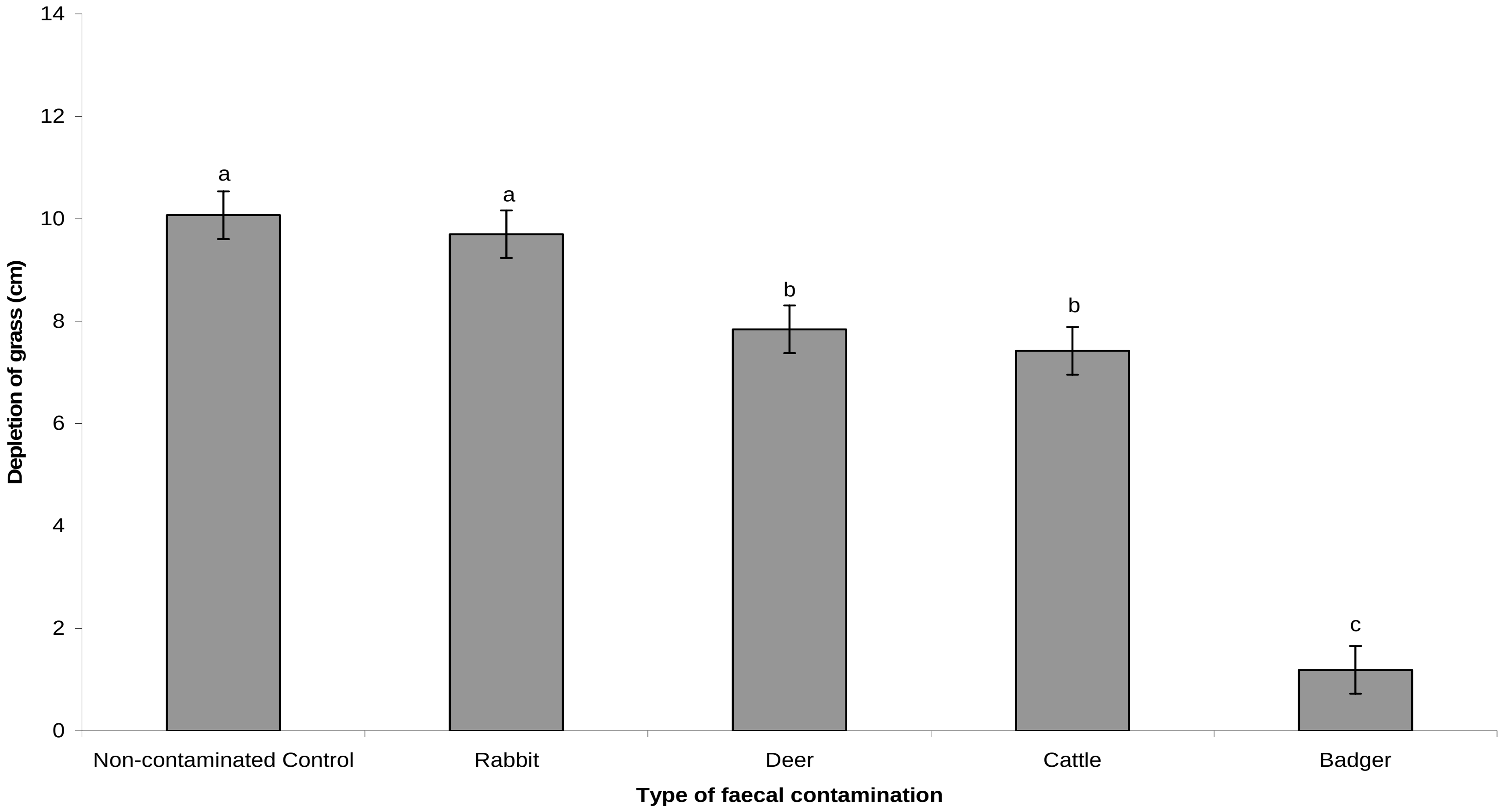

Fig. 2: Effect of path treatment (type of faecal contamination) in the type of faeces trial, on grass depletion (cm) by cattle. Figures are mean SSH per patch treatment at day 0 – mean SSH per patch treatment at day 12, ± SE. Letters donate significant differences between patch treatments.

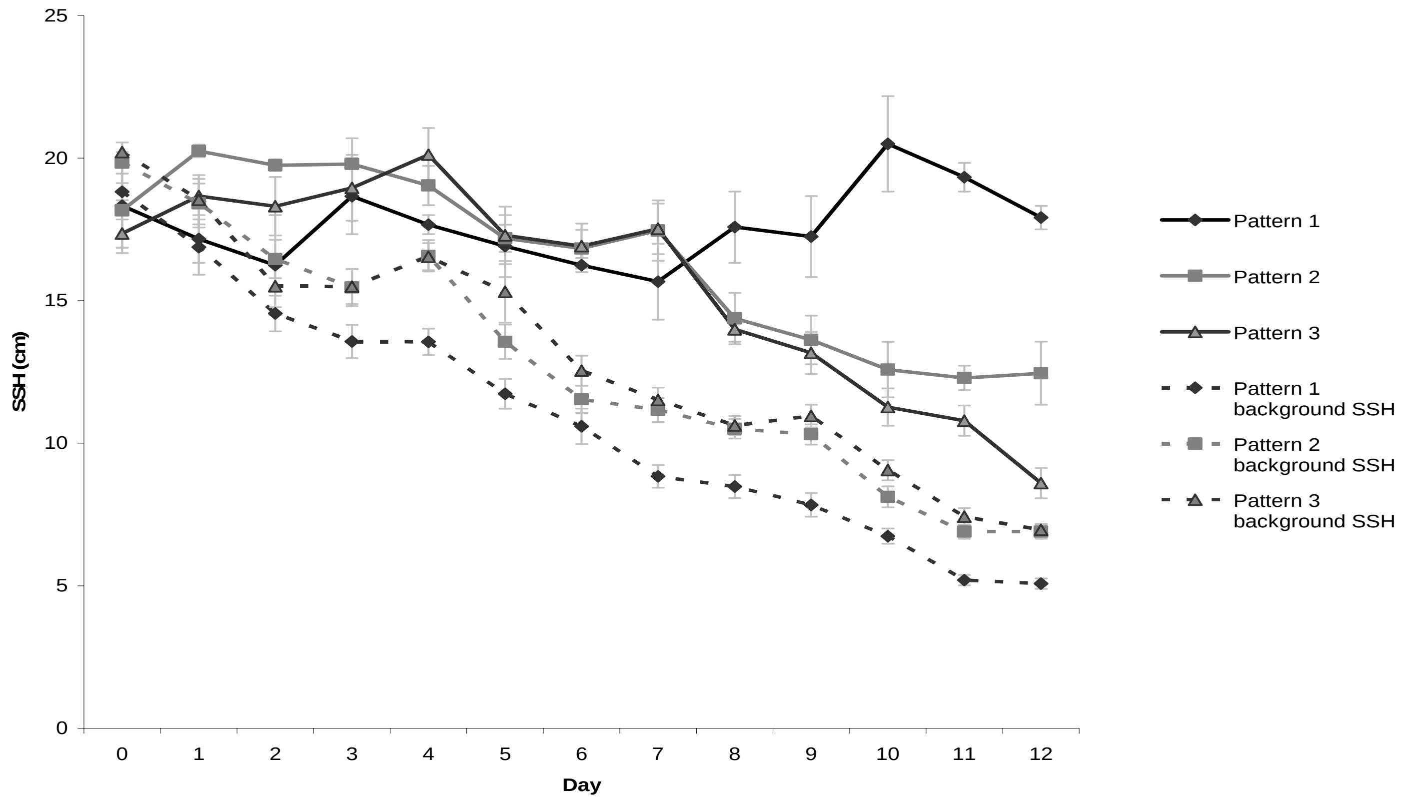

Fig.3: Effect of faecal pattern/concentration in the pattern of faeces trial, on SSH at the treatment patch and background SSH of the plot. Pattern 1 = one patch contaminated with 960g of badger faeces, Pattern 2 = two patches contaminated with 480g of badger faeces, Pattern 3 = four patches contaminated with 240g of badger faeces. Figures are the mean SSH per patch treatment, per day ±SE, and the mean background SSH per treatment, per day ±SE.

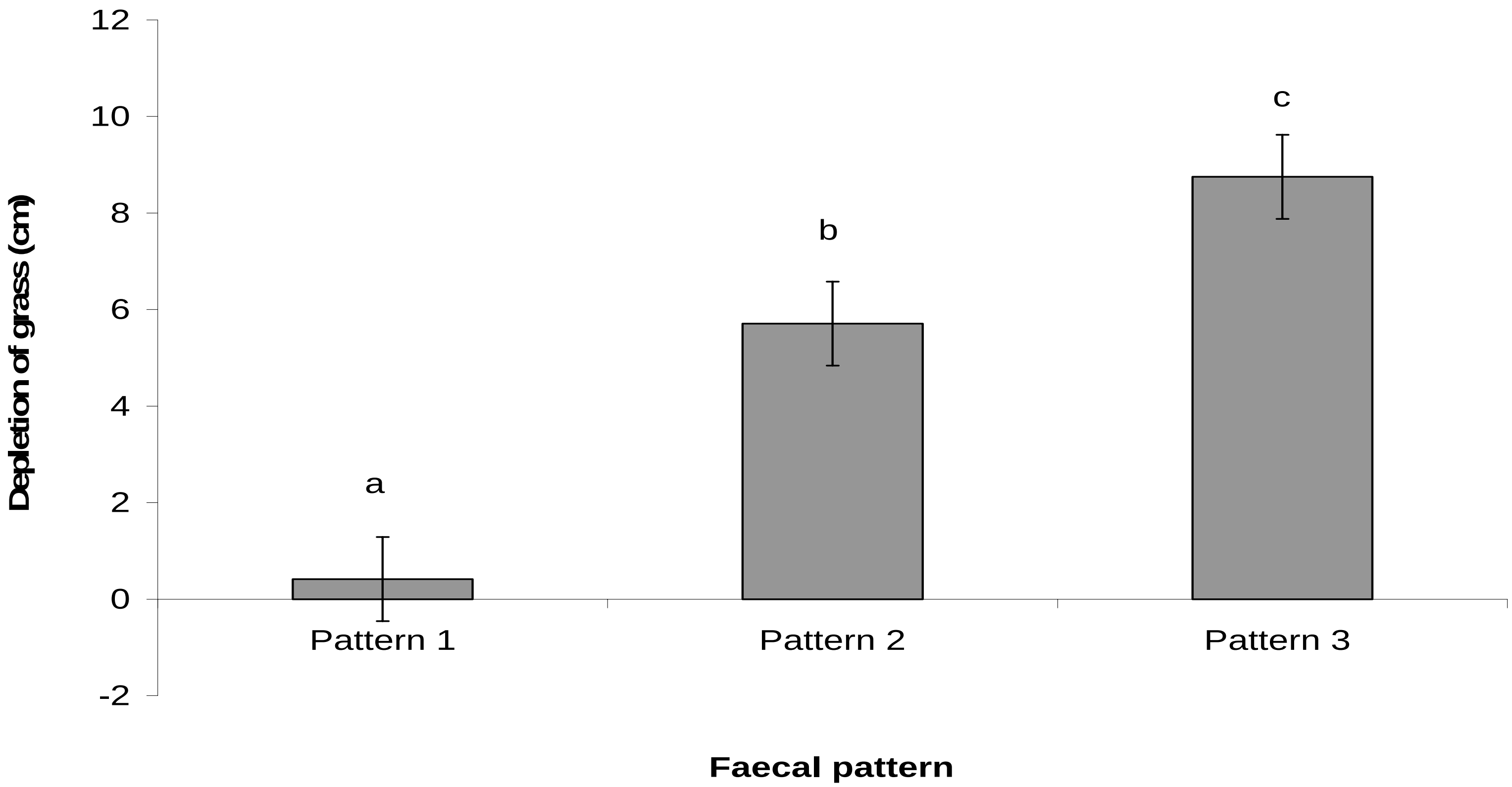

Fig. 4: Effect of faecal pattern/concentration in Exp 2, on grass depletion by cattle. Pattern 1 = one patch contaminated with 960g of badger faeces, Pattern 2 = two patches contaminated with 480g of badger faeces, Pattern 3 = four patches contaminated with 240g of badger faeces. Figures are mean SSH per treatment pattern at day 0 – mean SSH per treatment pattern at day 12, ± SE. Letters donate significant differences between patch treatment.