Effect of the nutritional environment and reproductive investment on herbivore–parasite interactions in grazing environments

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Parasitism is a serious challenge to herbivore health and fitness. To avoid parasites, herbivores avoid grazing near feces, creating a mosaic of contaminated tall avoided areas (tussocks) and noncontaminated short grazed areas (gaps). The mosaic represents a nutrition versus parasitism trade-off in that feces-contaminated tussocks are localized concentrations of both forage resources and parasites. Here, we use a grazing experiment with a natural tussock–gap mosaic to determine how the nutritional environment and reproductive effort affect sheep grazing decisions when faced with this trade-off. There were 3 animal treatments (barren ewes, ewes suckling a single lamb, and ewes suckling twin lambs) and 2 environment treatments (low and high nitrogen). Sward selection and grazing behavior were measured using focal observations on grazing ewes. Sheep showed an overall strong and significant avoidance of tussocks across all treatments. However, there was a reduction in the avoidance of tussocks by ewes on the low-nitrogen (low-N) plots. Ewes suckling twins showed a reduced avoidance of tussocks compared with barren ewes. Lactating ewes in low-N environments further reduced their avoidance of tussocks. Ewes with twins, which are at greatest risk from parasites, had the greatest contact with feces and thus parasites, especially in low-N environments. We conclude that twin-bearing ewes accept the increased risk of parasitism in order to gain the nutrients required to support increased reproductive effort, thus increasing their investment in current offspring at the cost of increased risk of parasitism and thus future potential reproductive attempts. Key words: feces avoidance, fitness, grazing, maternal investment, parasite risk.

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Thus, the mosaic represents a nutrition versus parasitism trade-off in that the feces-contaminated tussocks are localized concentrations of both nutritional resources and parasites (Hutchings et al. 2000; Hutchings, Kyriazakis, and Gordon 2001). Grazing decisions in relation to the gap and tussock mosaic will determine herbivore intake of nutrients and parasites and thus fitness and survival. Herbivore grazing behavior might be expected to reflect the costs and benefits of the trade-off, which are determined by both animal (e.g., physiological state) and environmental factors (e.g., forage availability) (Hutchings et al. 1999). In nutrient-rich environments, for example, fertilized agricultural pastures, the nutrient input from feces might be expected to have little effect on the nutritional content of the surrounding swards (Haynes and Williams 1993). In contrast, in nutrient-poor environments, for example, natural or extensive systems, nutrient leaching from feces may cause a significant increase in the nutritional value of the surrounding swards compared with the rest of the field (Edwards and Hollis 1982). Therefore, herbivores might be expected to adopt different grazing strategies in different environments.

Lactation is one of the most nutritionally and energetically demanding activities of female herbivores (Thornton 1987), and high maternal investment during this period can have an effect on female body condition and subsequent reproductive performance (Clutton-Brock 1991). The energy requirements of herbivores increase with increasing number of offspring (Agricultural and Food Research Council 1993). Therefore, it is possible that increased nutritional demand (via lactation) may result in grazing animals increasing their exposure to and risk of parasitism in order to gain the nutritional benefits associated with feces-contaminated tussocks. However, lactating animals also experience a periparturient relaxation in acquired immunity (ppri) (Barger 1993) and are therefore...
more susceptible to parasites during the period of increased nutrient demand. Thus, lactating herbivores may face a heightened dilemma in terms of the trade-off, that is, do they favor current reproductive attempts accepting greater exposure to parasites in order to maximize nutrient intake to the potential detriment of future fitness or vice versa?

Here we determine the impact of nutritional environment and level of maternal investment on sheep grazing decisions when faced with a nutrition versus parasitism trade-off. Specifically, we test the hypotheses: 1) sheep will reduce avoidance of feces-contaminated tussocks and thus take greater risks of parasitism in low-nutrient environments, 2) sheep with increasing lamb numbers (and thus increasing nutrient demand) will show decreased avoidance of tussocks, and 3) there is an interaction between hypotheses (1) and (2) in that increasing reproductive effort in low-nutrient environments will lead to further reductions in avoidance of feces-contaminated tussocks.

METHODS

Experimental design

The experiment was conducted in spring 2004 on a 1.5-ha experimental field plot, which was divided into six 0.25-ha plots. There were 2 environmental treatments and 3 animal treatments. The environment treatments consisted of a high-nitrogen (high-N) treatment and a low-nitrogen (low-N) treatment. Prior to the start of the experiment, the environment treatments were created by fertilizing half the plots to create a high-N treatment (ammonium nitrate applied at a rate of 40 kg N/ha), and half the plots were left unfertilized to create a low-N treatment (no fertilizer for 12 months). There were 3 plots per treatment. The plots were then grazed by a pool of 57 Grayface ewes and their lambs, managed to create a natural gap/tussock mosaic according to the protocol detailed in Hutchings, Gordon, et al. (2002). The 3 animal treatments consisted of ewes in different reproductive states: barren ewes, single-bearing ewes, and twin-bearing ewes. Each treatment had 6 ewes, divided into 2 groups. Once the mosaic was created, the experiment took place over a period of 12 days. In order to minimize any effect of plot differences on diet selection, each group of ewes was moved antclockwise around the plots on a daily basis. Thus, each group of ewes experienced each plot twice over the course of the experiment.

Animals

Eighteen Scottish Grayface ewes were selected randomly from a commercial flock and divided into 3 animal treatments according to reproductive effort: barren ewes with no lambs (live mean weight 79.18 ± 3.71 kg [mean ± SE]), single-bearing ewes (77.68 ± 1.55 kg), and twin-bearing ewes (71.02 ± 3.15 kg). All animals were treated with cydectin oral drench prior to the start of the experiment as part of normal parasite-control strategies. Fecal egg counts (number of parasite eggs excreted per gram of sheep feces), carried out on the animals before the experiment, confirmed that all animals possessed negligible parasite burdens.

Sward measurements

On days 1, 7, and 12, sward surface height (SSH) and tussock availability were measured, and composite mean sward samples were collected for chemical analysis. Stratified sward height measurements were measured using a sward stick (Barthram 1985) from both feces-contaminated tussocks and noncontaminated gap swards along a W-transect. Tussock availability was determined by walking a W-transect in each plot and recording which vegetation type (gap/tussock) was present at the toe of each step following the protocol described in Hutchings, Milner, et al. (2002). Composite mean sward samples (approximately 100 g) were collected separately for gap and tussock vegetation for each plot. Each sample was dried in a hot air oven to provide a dry matter (DM) estimate that was analyzed for nitrogen content and % digestive organic matter in dry matter (DOMD) using near-infrared spectroscopy. At the end of the experiment, 500 random pluck samples of gap vegetation and 500 pluck samples of tussock vegetation were taken from each plot, using thumb and forefinger to estimate the relative amount of herbage that would be consumed by the sheep when grazing the different sward types. The pluck samples were pooled into composite means for gap and tussocks of each treatment (high N/low N), which were analyzed for nitrogen and DOMD as above.

Animal grazing behavior and sward patch selection

Grazing behavior was measured by one observer from 1 of 2 observation towers overlooking the experimental plots 5 m above ground level, using direct observations on randomly selected individuals for a 5-min period of activity. All individuals were recorded twice a day giving a total of 432 focal observations of 5 min each over the 12-day period. The following grazing variables were recorded during each observation.

1. Number of bites taken from tussocks and gaps. A bite was defined as a head pull associated with the severing of herbage (Newman et al. 1992).
2. Bite rate (bites per second).
3. Step rate (steps per second). A step was defined as the forward motion of a chosen front leg.

Statistical analysis

Sward treatment effects (high N/low N) and sward-type effects (gap/tussock) were analyzed using analysis of variance (ANOVA) on SSH (cm), nitrogen content (g/kg DM), and DOMD using plot and sampling period as a block term in the ANOVA structure. Ivlev’s electivity index (IV) (Krebs 1989) was used to determine whether animals selected or avoided tussocks while grazing. IV values were produced using the formula IV = (O - E) / (O + E) (where O = observed proportion of bites taken from tussock areas and E = observed proportion of tussock area available). The IV values range from -1 to +1, which corresponds to rejection and selection respectively. Residual maximum likelihood (REML; Patterson and Thompson 1971) was used to estimate the mean values for grazing parameters (proportion of bites taken from gaps/tussocks, bite rate, step rate, and IV value). The GENSTAT REML procedure (Laws Agricultural Trust 1993) was used to estimate SEs and SEs of the differences. The model included animal, plot, and their interactions as fixed effects. Due to social facilitation, it is possible that step rate may not be independent of group composition and variances associated with this variable may be underestimated (Rook and Penning 1991). However, the effects of social facilitation have been found to be generally small (Rook 1998). The Wald test from the REML model was used to determine significant differences, with the Wald statistic (W) presented with the relevant degrees of freedom and probability value for the fixed effects of the REML model (Laws Agricultural Trust 1993). The data for the proportions of bites taken from gaps and tussocks were arcsine transformed before use in parametric statistical analysis (Zar 1984). Arcsine-backtransformed proportion means are presented with upper and lower 95% confidence limits.
RESULTS

Environmental measurements

The overall proportion of tussock area [backtransformed mean (with upper and lower 95% confidence interval)] was 0.23 (0.20–0.27). There was less tussock area in the low-N plots compared with high-N plots, with the proportions of available area (backtransformed mean [with upper and lower 95% confidence interval]) being 0.17 (0.16–0.18) and 0.30 (0.29–0.31), respectively. Overall, tussocks across all treatments had a greater SSH than gap swards (F_{1,12} = 5330.95, P < 0.001) (Table 1). There was an environment effect on the SSH of all plots, with high-N plots having a greater SSH than low-N plots (F_{1,12} = 20.03, P < 0.05) (Table 1). Nitrogen content was greater in tussocks compared with gap swards (F_{1,12} = 176.00, P < 0.001) (Table 1). There was an interaction between nitrogen treatment and sward type on the nitrogen content of gaps, with a greater difference between the nitrogen content of gaps and tussocks in the low-N plots compared with the high-N plots (F_{1,12} = 22.31, P < 0.001) (Table 1). There was no effect of nitrogen treatment (F_{1,12} = 7.54, P > 0.05), sward type (F_{1,12} = 1.34, P > 0.1), or their interactions (F_{1,12} = 2.64, P > 0.1) on DOMD (Table 1). Five hundred pluck samples of gap and tussocks in each of the low-N plots produced 113.21 g of fresh matter (FM) and 29.5 g of DM from the tussock swards. The high-N plots produced 178.0 g of FM and 42.2 g of DM for gap swards compared with 527.7 g FM and 102.3 g of DM from the tussock swards. The high-N plots produced 113.21 g of fresh matter (FM) and 29.5 g of DM from the gap swards compared with 527.7 g FM and 102.3 g of DM from the tussock swards. The high-N plots produced 178.0 g of FM and 42.2 g of DM for gap swards, whereas tussock swards produced 718.3 g FM and 150.1 g DM. Thus, tussocks potentially offered grazing sheep 4 times the FM intake compared with gap swards.

Sheep sward selection and grazing behavior

The nutritional environment affected the sward selection of the ewes (Table 2). Ewes in low-N plots took a higher proportion of their bites from tussock swards (W = 73.35, df = 1, P < 0.001), despite the relatively low tussock availability. Ewes with increasing reproductive effort took a higher proportion of their bites from tussock swards (W = 40.33, df = 2, P < 0.001). There was an interaction between reproductive effort and nutritional environment, ewes with twin lambs in low-N plots taking disproportionately more bites from tussocks compared with ewes suckling single lambs and barren ewes (W = 6.74, df = 2, P < 0.05) (Table 2). Using the IV, which shows tussock selection in relation to availability (i.e., translating bites from tussocks into selection or avoidance), sheep showed an overall strong and significant avoidance of tussocks across all treatments (Figure 1). However, there was a significant reduction in the avoidance of tussocks by animals on the low-N plots (W = 29.73, df = 1, P < 0.001). Ewes suckling twins showed significantly reduced avoidance of tussocks compared with barren ewes (W = 30.98, df = 2, P < 0.001). The reproductive effort × environment interaction was also apparent with ewes suckling twins in low-N environments showing the least avoidance of tussocks (W = 6.49, df = 2, P < 0.05) (Figure 1). There was a significant animal treatment effect on bite rates (Table 2) with ewes suckling single

Table 1

<table>
<thead>
<tr>
<th>Sward type</th>
<th>High-N</th>
<th>Low-N</th>
<th>Effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>SSH</td>
<td>Gap</td>
<td>3.17</td>
<td>2.43</td>
</tr>
<tr>
<td></td>
<td>Tussock</td>
<td>11.02</td>
<td>9.07</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>Gap</td>
<td>26.49</td>
<td>18.28</td>
</tr>
<tr>
<td></td>
<td>Tussock</td>
<td>37.74</td>
<td>41.97</td>
</tr>
<tr>
<td>DOMD</td>
<td>Gap</td>
<td>78.67</td>
<td>77.22</td>
</tr>
<tr>
<td></td>
<td>Tussock</td>
<td>78.44</td>
<td>78.33</td>
</tr>
</tbody>
</table>

RESULTS

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Table 2

<table>
<thead>
<tr>
<th>Plot treatment</th>
<th>High-N</th>
<th>Low-N</th>
<th>Treatment effects</th>
</tr>
</thead>
<tbody>
<tr>
<td>Animal treatment</td>
<td>B</td>
<td>S</td>
<td>T</td>
</tr>
<tr>
<td>Bite rate (bites per second)</td>
<td>0.92</td>
<td>0.95</td>
<td>0.94</td>
</tr>
<tr>
<td>Step rate (step per second)</td>
<td>0.089</td>
<td>0.083</td>
<td>0.086</td>
</tr>
<tr>
<td>Proportion</td>
<td>0.017</td>
<td>0.041</td>
<td>0.051</td>
</tr>
</tbody>
</table>

B = barren ewes, S = ewes suckling a single lamb, SED = standard error of the difference, and T = ewes suckling twin lambs. Values given are means of bite rates, step rates, and backtransformed mean proportion of bites from tussocks (with upper and lower 95% confidence limits). NS = P > 0.05, * P < 0.05, *** P < 0.001.
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DISCUSSION

The aim of this experiment was to determine how the nutritional environment and level of maternal investment affect sheep grazing behavior in relation to environmental distributions of forage resources and feces/parasites. The first step in this study was to create the heterogeneous sward mosaic representing the nutrition versus parasitism trade-off. The feces-contaminated tussocks in both the high-N and low-N plots had significantly greater SSH than the gap swards, thus a heterogeneous sward structure had been created. As expected, the application of nitrogen fertilizer resulted in an increased nitrogen content in the gap swards of the high-N plots compared with low-N plots. The similar nitrogen content of tussocks in both the nitrogen environments, coupled with the higher nitrogen content of gaps in the high-N environment, resulted in a greater difference between the tussocks and gaps in the low-N environments than in the high-N ones. The pluck samples showed that tussocks provided grazing herbivores with a greater forage intake per bite compared with gap swards. However, the tussocks contained feces that is strongly avoided as it is used as a cue by the animals to the presence of parasites (Cooper et al. 2000). Sward larval counts (numbers of infective stage parasites in swards and thus parasite intake) increase with increasing amounts of fecal contamination (Hutchings et al. 1998). Indeed, tussocks in this type of mosaic in both agricultural (established using the same methods as here) and natural systems contain a greater risk of parasitism with increased levels of infective stage parasite larvae (up to 5.5 times greater number of parasite larvae per gram of DM) compared with gap swards as previously quantified in Hutchings, Gordon, et al. (2002) and Hutchings, Milner, et al. (2002). Tussock avoidance by grazing herbivores significantly reduces their parasite intake (Michel 1955; Cabaret et al. 1986). Thus, the ewes faced the dilemma of adapting a behavioral strategy to maximize nutrient intake (selecting tall tussocks) and minimize parasite exposure (avoidance of feces). This trade-off dilemma was further heightened in the low-N plots as the nutritional advantage of grazing tussocks in low-N plots increases.

The environmental treatments in this experiment may be seen as representative of both agricultural and natural systems. Agricultural systems can range from high-input intensive systems to low-input extensive grazing systems, whereas natural systems are likely to be relatively nitrogen poor. Thus, both domestic and wild grazing herbivores must make foraging choices based on the trade-off described above and can be seen as being in a state of conflict regarding these choices (Hutchings, Gordon, et al. 2002).

Whereas all animals in this experiment maintained a degree of avoidance to fecal-contaminated tussocks, both the nutritional environment and reproductive effort of the ewes affected the degree of aversion toward tussocks. These results are consistent with the idea that fecal avoidance in grazing herbivores is a strong and inherent behavior (Hutchings et al. 1998) and suggests that, in general, the perceived costs of grazing tussocks outweigh the nutritional benefits.

In terms of the nutritional environment, the increased selection for tussocks in low-nutrient environments can be attributed to the greater difference in nitrogen content between the gaps and tussocks in the low-N plots compared with high-N plots. This will have increased the benefits of grazing tussocks in low-N environments. Additionally, in low-N environments, step rate increases, possibly due to the lower tussock area and thus a greater distance between tussocks. This grazing behavior in low-quality environments suggests that the nitrogen leaching from feces into swards is selected by ewes irrespective of their reproductive status/effort to meet their nutrient requirements and that ewes are prepared to take the increased risk of parasitism to achieve intake goals. Thus, the nutritional environment appears to affect the grazing decisions of the ewes and thus their exposure to parasites/pathogens by altering the costs and benefits of grazing feces-contaminated tussocks.

In extreme environments, parasitism has deleterious effects on reproduction by decreasing fecundity and neonate survival (Gulland 1995). However, the results observed here suggest that ewes with a greater number of offspring (reproductive effort) will increase their exposure to and risk of parasitism by reducing avoidance of feces. The nutritional requirements of ewes are at the highest during lactation (Bocquier et al. 1987). Nutrient demand also increases with the number of offspring due to milk production, for example, feeding requirements increase to twice that of maintenance for single-rearing ewes and 3 times maintenance for twin-rearing ewes (Kerr 2000). Thus the greater tussock selection by ewes with twins is likely to be due to ewes with twin lambs needing to increase their nutritional intake and having to accept the parasitism costs of grazing tussocks in order to gain the nutritional benefits. Furthermore, not only are the lactating ewes taking a greater risk of exposure to parasitism in terms of forage choice, but they are also more susceptible to parasites during this period. The occurrence of ppri (e.g., a breakdown of immunity in lactating animals results in increased susceptibility to parasitism during this time (Barger 1993), with twin-bearing ewes having a greater breakdown of immunity than single-bearing ewes (Houdijk et al. 2001). The extent of this breakdown is linked to nutrient intake, with a greater parasite susceptibility occurring when metabolizable (available) protein is scarce (Houdijk et al. 2001). The food intake of grazing animals is affected by herbage availability, with relatively severe restrictions in herbage intake occurring in sheep on pasture with sward heights of 3 cm (Penning et al. 1991). Thus, in this experiment where the overall mean sward height of non-contaminated gap swards was below 3 cm, nutrient intake was likely to be restricted. Furthermore, immunity in lactating animals is not fully restored until the offspring are weaned (O’Sullivan and Donald 1970, 1973), suggesting that the lactating animals in this experiment were indeed more susceptible to parasitism than the nonreproducing (dry) animals.
Previous studies have shown that parasitized animals tend to reduce the risk of further parasitism by increasing avoidance of feces-contaminated vegetation (Hutchings et al. 1999; Hutchings, Milner, et al. 2002), whereas immune animals reduce avoidance of feces as they are at less risk from parasites (Hutchings et al. 1999; Hutchings, Gordon, et al. 2001). In contrast, here lactating animals that are likely to be experiencing a breakdown of immunity are taking a greater risk of parasitism and thus potentially a greater cost to their own future fitness in order to increase nutrient intake. The increased risk of parasitism by lactating ewes can be considered a form of parental investment. Investment in reproduction by parasitized animals has previously been considered on a nutritional basis within a nutrient-partitioning framework (Coop and Kyriazakis 1999; Houdijk et al. 2001). This framework suggests that animals prioritize maintenance functions (those associated with short-term survival) and reproductive effort over immunity. Thus, lactating animals allocate scarce nutrients to these functions at the cost of immunity. The behavior of the lactating ewes in this experiment indicates that the ewes not only prioritize reproductive effort in terms of nutrient allocation but also behaviorally in terms of their diet choice, with ewes supporting twin lambs choosing a foraging strategy with potentially greater future fitness costs. This is consistent with the theory of parental care strategies in which parental investment increases with offspring number (Clutton-Brock 1991).

In conclusion, both the nutritional environment and the reproductive status of herbivores have an effect on an individual’s grazing behavior in relation to environmental distributions of feces and thus parasites. Grazing animals maintain an overall avoidance of feces, but the degree of this avoidance is linked with the relative costs and benefits to the individual of grazing feces-contaminated herbage. In low-N environments, ewes suckling twins showed the greatest reduction in avoidance of feces and therefore the greatest exposure to and risk of parasitism. Thus, in environments where nutrients are relatively scarce, ewes with high reproductive costs via number of offspring may be increasing investment in current reproductive events over future potential reproductive events. This study has shown that the nutritional environment and reproductive effort have an effect on the grazing decisions of herbivores in relation to heterogeneous distributions of forage resources and feces and thus parasites that in turn have potential implications for future fitness and survival.

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