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# Effects of human disturbance on the diet composition of wild red deer (*Cervus elaphus*)

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**Abstract** Disturbance from human recreational activities may affect the nutrition of free-ranging herbivores due to trade-offs between feeding in preferred habitats and perceived predation risk. To test this hypothesis, we estimated diet composition for red deer in the Scottish highlands in spring, when recreational activity tends to be high, and in winter when it is lower. We analysed faecal

samples from three habitat types (grassland, heather moorland and woodland) collected at sites close to a busy track (disturbed) and at a distance from it (less disturbed). The diet consisted of 39% grasses, sedges, herbs and rushes (GSHR) and 58% *Calluna vulgaris* and *Erica* spp. (heather) in spring, compared with 14% grasses and 77% heather in winter, with small quantities of *Vaccinium* spp. (berry) and *Pinus sylvestris* (tree) in both seasons. In spring, faeces from disturbed grass and woodland sites indicated a diet with less GSHR and more heather and tree than faeces from less-disturbed sites, which could be due to an increased need for vigilance in exposed grassland and the need to seek cover. In contrast, faeces from all disturbed sites in winter indicated a diet with more GSHR and less heather than faeces from less-disturbed sites. This could be due to a seasonal decline in recreation and increase in hunting activity reversing the disturbance levels at the different sites, since hunting is not normally carried out in areas used by the public for recreation. We conclude that there may be nutritional benefits to deer of reducing disturbance near open grassland.

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## Introduction

Herbivory, under natural conditions, reflects trade-offs between foraging and minimising predation risk. It is evident that choice of feeding patch (Newman and Caraco 1987) and behaviour within a patch (Krebs et al. 1991)

depend not only on the availability of food but also on many other factors, including the perceived level of predation risk, which may ultimately be reflected in the diet. The similarities between the responses elicited in wild herbivores to predators and to non-predatory human disturbance have led to the assumption that animals may perceive all human disturbance as a predation risk (Frid and Dill 2002) and, as such, human disturbance could have important effects on habitat selection and diet composition (Lima and Dill 1990; Frid and Dill 2002). Indeed, daytime browsing of tree bark by red deer has been associated with disturbance in areas where hunting is practised, posing an increasing threat to forests (Rajsky et al., 2008).

Three distinctive and ubiquitous habitats frequented by red deer (*Cervus elaphus* L.) in Scotland are heather moorland, grassland and woodland (Watson and Staines 1978; Clutton-Brock and Albon 1989; Hester et al. 1999). Around 60% of the Highland Region of Scotland consists of semi-natural heather moorland and peatland, around 10% consists of mostly coniferous woodland and less than 10% of grassland, with the complexity of the landscape reflected in the predominance of mosaic features (LCS 88, MLURI 1993). The heather moorland is dominated by *Calluna vulgaris* L. Hull with some *Erica* spp., while grassland provides higher quality and preferred forage for red deer (Milne et al. 1978; Clutton-Brock et al. 1982) with *Agrostis/Festuca*, *Molinia*, *Nardus*, *Carex* and *Juncus* spp. being the most common. The woodland consists mostly of coniferous trees, such as *Pinus* and *Larix* spp., with some broadleaved species such as *Betula* and *Salix* spp. and commonly contains a mixed grass and *Vaccinium* spp. understorey. *Vaccinium myrtillus* is also abundant in some areas of heather moorland and, to a lesser extent, in grassland. It is common for the feeding grounds of the red deer to be disturbed by human recreational activities in spring and summer (Staines and Scott 1994) and by hunting in autumn and winter (Bullock et al. 1999). Both types of disturbance have been shown to increase vigilance by red deer, particularly in grassland habitats (Jayakody et al. 2008), as deer may be more prone to disturbance in grassland where they are more exposed (Jayakody et al. 2008). The proportion of grass species in the diet could be affected by disturbance if animals have to move away from grassland into nutritionally poorer, less-preferred habitats in order to seek cover (Jayakody 2005). Since grassland species provide relatively high amounts of digestible organic matter in the growing season (Gordon 1989), even a small reduction in the percentage of grass species in the diet at this time of year could have consequences for animal performance if the time available for feeding is limited (White 1983).

Our aim in this study was to see whether we could detect differences in the diet composition of red deer subjected to different levels of disturbance by human recreational

activities, when feeding on Scottish upland vegetation. We hypothesised that red deer will have a lower percentage of grass in their diet in areas where the level of disturbance is relatively high. To test this hypothesis, we analysed faecal samples collected from different habitat types (grassland, heather moorland and woodland) in areas with different levels of recreational disturbance.

## Methods

### Study area

We carried out our study on the eastern side of the Cairngorm mountain range in the Highland Region of Scotland, within an area stretching from latitude 56°55'N to 57°03'N and from longitude 3°08'W to 3°23'W. The dominant vegetation types in the area are sub-montane vegetation and heather moorland on the higher ground, with coniferous woodland, grassland and wetland covering most of the lower altitude areas (Gimingham 2002a).

We categorised parts of the study area as 'disturbed' or 'less disturbed' from a combination of anecdotal information, historical data and reconnaissance surveys carried out to determine the numbers of people visiting for recreational or other purposes. Automatic counting equipment beside the main access track recorded an average of 264 visitors per day throughout the year, with 441 per day recorded over the summer months (June to August) during the 3 years prior to the study (G. Jones, unpublished data). The study area is popular for its amenity value, but the track also provides an access route into the mountains and is heavily used by hill-walkers and rock climbers. The majority of walkers stay on or close to the track until they get into the mountains so that the track provides a concentrated source of disturbance at lower levels. Areas within 500 m or so of the track were therefore categorised as 'disturbed', while areas of higher ground further away (>1,000 m) from the track were categorised as 'less disturbed'. Generally, no more than about 10 visitors per day are seen in the 'less-disturbed' areas (G. Jones, personal communication). During a series of 96 1-h observation periods carried out in the same study area in May and June 2003 (Jayakody et al. 2008), a mean ( $\pm$ SE) of 50 ( $\pm$ 7.8) visitors per hour were observed walking close to groups of deer in the disturbed areas, although no people were seen close to deer in the less-disturbed areas (S. Jayakody, unpublished data). Within each of these areas, a total of 12 sites were selected for sampling faeces, consisting of two replicate clusters of three disturbed sites and two replicate clusters of three less-disturbed sites, with each cluster consisting of one site in each of the three main habitat types (grassland, heather moorland and woodland).

Within replicates, the average distance between the grassland, heather moorland and woodland sampling sites was 0.75 ( $\pm 0.131$ ) km, while the average distance between replicates was 5.8 ( $\pm 0.86$ ) km.

#### Collection of faeces and forage samples

In wild free-ranging animals, diet composition analysis necessarily depends on remote faecal sampling. In this study, we used faecal concentrations of indigestible plant markers to estimate the proportions of different forage species in the diet (Dove and Mayes 1996). The method has been used successfully for wild herbivores in a number of studies, using *n*-alkanes (Hulbert et al. 2001; Bugalho et al. 2002; Martins et al. 2002a, b; Bugalho and Milne 2003; Rao et al. 2003) and long-chain fatty alcohols (Rao 2001; Ali 2003).

We collected red deer faeces samples during the last week of April 2003 (spring) and the last week of January 2004 (winter). At each sampling site, five parallel 50-m transects were laid, with the first transect starting from a randomly chosen point within the habitat type. Parallel transects were 40 m apart and faeces were detected visually when walking along each transect. We collected only fresh faecal pellets, which were identified by a visual inspection method (Jayakody 2005). Similar numbers of samples were collected in each habitat type, with a total of 61 samples from the disturbed areas and 30 from less-disturbed areas in spring, plus 21 samples from disturbed areas and 20 from less-disturbed areas in winter. We also sampled locally abundant plant species and species known to be consumed by red deer (Kay and Staines 1981; Fraser and Gordon 1997a; Latham et al. 1999), as well as any other plants showing evidence of recent grazing or browsing damage. The vegetation types found in the disturbed and less-disturbed sites were similar, with the grassland being dominated by *Molinia* spp., *Agrostis* spp., *Festuca* spp., *Deschampsia* spp., *Poa* spp., *Juncus* spp. and *Holcus* spp., the heather moorland by *Calluna vulgaris* and *Erica cinerea* and the woodland by *Pinus sylvestris* (Scots pine), *Larix decidua* (Larch) and *Betula pendula* (silver birch), with the understorey containing varying amounts of *Vaccinium myrtillus* (berry), *Calluna vulgaris* and *Erica* spp. (heather) and various grasses and herbs found in grassland. Due to die-back of most of the grass species in winter, we collected only a single sample of mixed grass species in January.

When sampling faeces, we collected all the pellets within a pile, taking care to minimise contamination from soil and plant material. When sampling forage, we collected plant material sufficient for generating approximately 2–3 g of freeze-dried matter. For the larger plants, the parts that are known to be consumed by deer were harvested. In the case of very small species, the entire above-ground biomass was harvested. We immediately

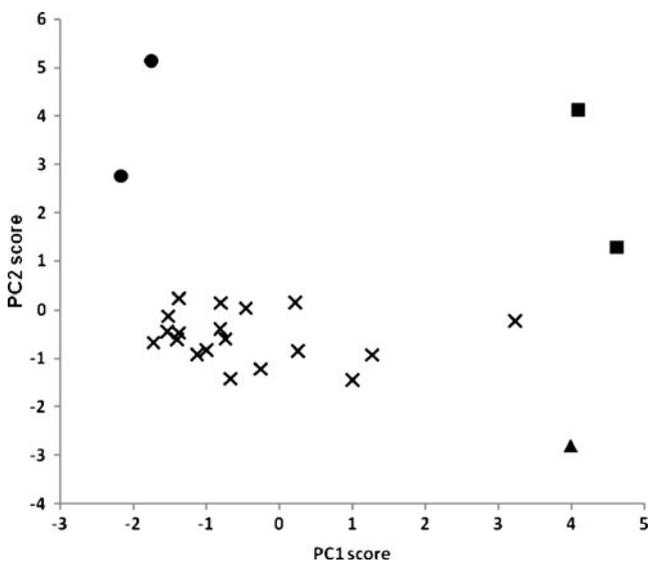
sealed all faeces and forage samples separately in air-tight polythene bags and stored them at  $-20^{\circ}\text{C}$  within 8 h of collection. Later, we freeze-dried the samples, milled them through a 1-mm mesh and analysed them for *n*-alkanes according to the method of Mayes et al. (1986), as modified by Ali et al. (2004), and for long-chain fatty alcohols according to the method of Ali et al. (2004). Because they are normally absent from forage species, or only present in very low concentrations, we used docosane ( $\text{C}_{22}$ ) and tetratriacontane ( $\text{C}_{34}$ ) as internal standards for *n*-alkane analysis and 1-heptacosanol ( $\text{C}_{27}$ ) as the internal standard for fatty alcohols.

#### Grouping of forage species

One of the main limitations in using *n*-alkane and fatty alcohol markers for estimating the composition of complex diets is the relatively low number of markers available in forage species, usually somewhere between 10 and 15 (Dove and Mayes 1996). Where diet composition is expected to be complex, forage species are usually grouped to avoid the number of diet components exceeding the number of markers (Bugalho et al. 2002; Martins et al. 2002a; Rao et al. 2003). In this study, we sampled 24 different forage species in spring and grouped them into forage types, namely ‘GSHR’ (grasses, sedges, herbs and rushes; see Tables 2 and 3), ‘heather’ (*C. vulgaris* and *Erica* spp.), ‘berry’ (*V. myrtillus*) and ‘tree’ (*P. sylvestris* and *L. decidua*). Grouping was carried out on the basis of both taxonomic information and similarities in marker profiles. The latter were assessed using a Principle Components Analysis (PCA), using marker concentrations as variables (for a full description of the method, see Rao et al. 2003). The first two principle components (PC1 and PC2) (Table 1), which explained 24% and 18% of the variation, respectively, showed heather, berry and tree species as distinct from the GSHR species (Fig. 1). *Carex* (the common sedge) was also separated from the other GSHR species by the PCA, but exploration of the data using the least-squares optimisation procedure for diet composition (see below) indicated that if *Carex* was included as a separate forage type, distinct from the other GSHR species, it accounted for less than 0.1% of the total diet. *Carex* was therefore included in the GSHR group. Although berry (*Vaccinium* spp. in Fig. 1) also accounted for a relatively small proportion of the diet (<2% in spring), it was treated as a separate component in our analyses since it is widely distributed across the grassland, heather moorland and woodland habitats and was separated from GSHR species by both PC1 and PC2. In winter, the forage types used were ‘grass’ (the single mixed species sample), ‘heather’ (*C. vulgaris*), ‘berry’ (*V. myrtillus*) and ‘tree’ (*P. sylvestris*). Marker profiles for the four spring forage types and the winter mixed species grass sample are shown in Tables 2 and 3.

**Table 1** Scores for the first two principle components (PC1 and PC2) from the Principal Components Analysis of spring forage samples, showing grouping into GSHR, heather, berry and tree forage types

	Forage samples	PC1	PC2
GSHR	<i>Agrostis</i> spp.	-1.724	-0.666
	<i>Anemone nemorosa</i>	0.224	0.159
	<i>Anthroxanthum odoratum</i>	-1.001	-0.828
	<i>Bellis perennis</i>	-0.453	0.042
	<i>Carex</i> spp.	3.237	-0.222
	<i>Deschampsia caespitosa</i>	-0.811	-0.387
	<i>Deschampsia flexuosa</i>	-0.735	-0.595
	<i>Festuca ovina</i>	1.270	-0.928
	<i>Holcus lanatus</i>	-0.665	-1.415
	<i>Juncus effusus</i>	-1.127	-0.918
	<i>Juncus squarrosus</i>	-0.255	-1.216
	<i>Luzula sylvatica</i> .	-1.373	0.241
	<i>Molinia</i> spp.	-1.400	-0.603
	<i>Nardus stricta</i>	-1.379	-0.469
	<i>Poa</i> spp.	0.262	-0.843
	<i>Potentilla erecta</i>	1.004	-1.443
	<i>Scirpus caespitosus</i>	-0.806	0.150
<i>Trifolium repens</i>	-1.536	-0.438	
<i>Viola</i> spp.	-1.523	-0.125	
Heather	<i>Calluna vulgaris</i>	4.096	4.126
	<i>Erica</i> spp.	4.630	1.284
Berry	<i>Vaccinium</i> spp.	3.991	-2.807
Tree	<i>Larix decidua</i>	-1.754	5.140
	<i>Pinus sylvestris</i>	-2.170	2.761



**Fig. 1** Two dimensional plot of Principal Component Analysis (PCA) of *n*-alkanes and longchain fatty alcohols for spring forage species, showing grouping into GSHR (crosses), heather (squares), berry (triangle) and tree (circles). The x axis indicates scores for Principal Component (PC) 1 and the y axis indicates scores for PC 2

#### Estimation of diet composition

Prior to estimation of diet composition in spring, we estimated the effective concentrations of *n*-alkane and long-chain fatty alcohols in the different forage types. This was done, for each forage type, by calculating the mean values for each individual *n*-alkane and long-chain fatty alcohol across all the component plant species. For both the spring and the winter samples, we corrected all *n*-alkane and fatty alcohol marker concentrations in the faeces for variation in faecal recovery rate. We used faecal recovery rates estimated for sheep (Ali 2003), as there were none available for red deer. We then calculated diet composition using concentrations of odd-chain *n*-alkanes within the range C<sub>21</sub>–C<sub>35</sub> and even-chain alcohols within the range C<sub>20</sub>–C<sub>34</sub> (spring samples) or C<sub>20</sub>–C<sub>30</sub> (winter samples) plus C<sub>29</sub> alcohol, which was present in very high concentrations in the tree species sampled (see Table 3). We used a least-squares optimisation procedure, described in detail by Dove and Mayes (2005), which determines the composition that gives the minimum value for the sum of the squared discrepancies between actual (faecal recovery-corrected)

**Table 2** The *n*-alkane concentrations (mg/g DM) for forage types used for diet composition calculations in spring and winter, and for the plant species grouped together as the GSHR forage type in spring

	C21	C23	C25	C27	C29	C31	C33	C35
Forage types—spring								
GSHR	2.0	3.8	6.8	20.5	76.1	119.1	61.7	4.1
Heather	4.6	3.5	15.0	42.9	113.3	539.6	277.5	5.2
Berry	2.3	6.2	29.3	72.7	186.2	120.0	17.5	1.3
Tree	1.5	1.7	1.3	1.5	2.3	1.4	1.9	1.2
Forage types—winter								
Grass	6.4	5.4	12.5	30.7	244.9	598.1	218.3	8.8
Heather	33.4	8.9	15.6	60.2	134.0	580.0	441.4	15.3
Berry	0.0	9.8	86.2	188.3	472.1	130.8	15.9	0.0
Tree	4.7	4.1	6.7	8.5	11.1	20.6	10.5	3.1
GSHR components								
<i>Agrostis</i> spp.	1.0	1.2	4.7	12.6	34.8	54.9	24.8	3.8
<i>Anemone nemorosa</i>	0.6	3.1	8.8	33.1	60.3	86.4	18.4	3.7
<i>Anthroxanthum odoratum</i>	2.2	5.7	6.0	17.0	24.3	22.6	20.6	10.3
<i>Bellis perennis</i>	1.6	2.0	11.5	14.8	57.9	139.8	28.3	6.6
<i>Carex</i> spp.	4.2	1.9	4.3	53.9	364.2	594.8	62.8	2.1
<i>Deschampsia caespitosa</i>	3.1	4.4	11.2	17.0	25.5	29.2	4.9	1.4
<i>Deschampsia flexuosa</i>	2.2	3.9	4.6	12.3	80.4	109.7	33.0	2.1
<i>Festuca ovina</i>	2.7	4.4	14.8	45.8	186.6	174.2	19.9	1.8
<i>Holcus lanatus</i>	3.9	8.8	7.6	7.6	11.1	18.9	16.5	2.8
<i>Juncus effusus</i>	0.8	1.2	1.6	11.6	178.6	42.7	1.8	1.2
<i>Juncus squarrosus</i>	1.3	1.1	1.2	3.6	35.1	226.6	29.9	1.7
<i>Luzula sylvatica</i>	1.1	2.4	3.1	10.0	22.3	14.9	5.5	1.9
<i>Molinia</i> spp.	2.3	2.0	4.7	10.2	27.7	56.2	26.0	3.9
<i>Nardus stricta</i>	1.1	4.9	2.6	6.7	64.3	45.7	11.0	1.9
<i>Poa</i> spp.	4.2	5.0	8.1	23.4	99.1	98.0	40.0	4.0
<i>Potentilla erecta</i>	1.3	11.1	6.1	39.3	84.7	94.2	63.6	3.3
<i>Scirpus caespitosus</i>	2.8	3.6	5.0	9.4	26.3	17.5	9.5	4.2
<i>Trifolium repens</i>	0.8	1.6	6.6	8.0	25.0	13.1	4.4	2.1
<i>Viola</i> spp.	1.4	2.1	3.5	11.0	40.6	37.5	7.3	1.4

and calculated faecal marker concentrations, according to the function:

$$\text{Minimise: } \sum (calculated\ marker_i - actual\ marker_i)_{alkane1-n}^2$$

Where, for a four-component dietary mixture:

$$Calculated\ marker_i = \alpha A_i + \beta B_i + \gamma C_i + \delta D_i$$

The values  $\alpha$ ,  $\beta$ ,  $\gamma$  and  $\delta$ , considered as unknowns, are the respective intakes of dietary forage types A, B, C and D, calculated to produce 1 kg of dry faeces. The constants  $A_i$ ,  $B_i$ ,  $C_i$  and  $D_i$  are the recovery-corrected faecal concentrations of marker<sub>*i*</sub> for the four forage types. Thus, for forage type A:

$$Dietary\ proportion\ of\ A = \frac{\alpha}{\alpha + \beta + \gamma + \delta}$$

Substituting  $\alpha$  by  $\beta$ ,  $\gamma$  or  $\delta$  as the numerator would give the dietary proportions of the other forage types. The Solver routine in Excel (Microsoft Office 2003) was used to carry out these computations.

#### Estimation of habitat availability

We based habitat availability estimates on detailed vegetation cover data from the Land Cover of Scotland 1988 dataset (LCS 88, MLURI 1993), in which land cover features were interpreted from aerial photographs at a scale of 1:24,000. We combined the various land cover classes identified in this dataset to produce six major categories: grassland, heather moorland, woodland, montane vegetation, peatland and water. We estimated the areas of grassland, heather moorland and woodland considered to be 'available' to the deer visiting each of the sampling sites, on the basis of previous measurements of the average home-range size for deer in a neighbouring herd (approximately 970 ha) in winter and spring (Sibbald et

**Table 3** The long-chain fatty alcohol concentrations (mg/g DM) for forage types used for diet composition calculations in spring and winter, and for the plant species grouped together as the GSHR forage type in spring

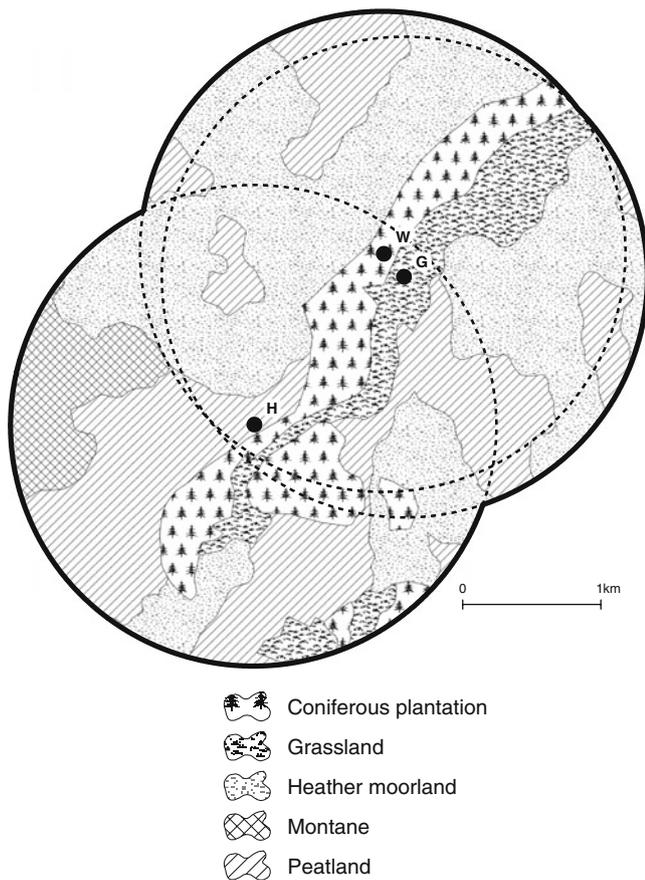
	1-C20-ol	1-C22-ol	1-C24-ol	1-C26-ol	1-C28-ol	10-C29-ol	1-C30-ol	1-C32-ol	1-C34-ol
Forage types—spring									
GSHR	22.1	74.0	122.9	553.3	817.2	24.4	407.7	63.1	25.1
Heather	77.2	427.3	372.0	255.3	287.1	88.5	397.1	71.3	32.8
Berry	61.1	112.1	219.4	347.4	520.5	5.5	1,222.2	213.7	21.6
Tree	111.5	328.3	114.5	54.4	62.0	1,866.8	126.7	24.4	4.8
Forage types—winter									
Grass	32.7	86.5	120.0	1,865.9	497.8	138.3	186.9		
Heather	139.5	700.1	360.6	113.2	138.1	16.0	427.7		
Berry	39.6	53.7	138.5	423.1	723.6	35.4	1,620.9		
Tree	102.6	356.9	156.5	80.4	96.0	1,436.3	90.1		
GSHR components									
<i>Agrostis</i> spp.	9.7	28.8	31.1	444.4	3,072.0	18.5	388.7	19.0	14.9
<i>Anenome nemorosa</i>	7.3	39.1	661.0	608.2	140.3	35.7	145.4	9.5	12.9
<i>Anthroxanthum odoratum</i>	0.0	33.7	112.6	94.0	3,599.1	15.7	218.2	18.9	10.6
<i>Bellis perennis</i>	32.3	36.7	36.8	145.8	107.5	35.7	200.0	39.7	16.9
<i>Carex</i> spp.	33.5	47.1	168.8	360.1	487.3	8.4	130.6	120.9	26.2
<i>Deschampsia caespitosa</i>	36.3	40.7	58.5	542.2	2,074.6	7.9	75.5	20.8	5.4
<i>Deschampsia flexuosa</i>	7.8	44.5	31.7	509.6	302.8	179.3	882.4	41.8	14.8
<i>Festuca ovina</i>	24.8	83.3	72.2	771.0	771.3	9.3	456.2	59.6	6.3
<i>Holcus lanatus</i>	0.0	33.1	61.9	3,408.7	190.1	15.3	78.3	11.4	15.4
<i>Juncus effusus</i>	0.0	6.9	13.1	113.0	58.2	20.8	321.2	121.3	15.9
<i>Juncus squarrosus</i>	4.1	5.6	15.3	46.1	43.3	10.3	115.2	305.7	149.5
<i>Luzula sylvatica</i>	11.7	110.9	261.7	136.8	230.0	3.3	360.5	35.1	5.3
<i>Molinia</i> spp.	9.2	28.2	29.4	414.4	2,479.8	0.0	388.2	39.0	17.3
<i>Nardus stricta</i>	14.9	83.3	38.9	39.3	88.1	0.0	999.8	15.8	6.0
<i>Poa</i> spp.	9.6	16.3	59.2	1,782.9	296.1	7.4	116.6	28.5	18.9
<i>Potentilla erecta</i>	27.4	39.5	123.7	325.2	623.1	11.0	451.3	135.6	64.2
<i>Scirpus caespitosus</i>	29.6	78.1	276.2	473.3	958.0	20.1	739.9	27.6	6.1
<i>Trifolium repens</i>	25.4	54.2	78.9	171.1	83.9	16.6	1,693.5	27.3	0.0
<i>Viola</i> spp.	9.3	61.8	91.1	340.0	321.7	45.1	165.8	26.9	8.7

al., unpublished data). This was done by drawing a circle of radius 1,757 m around each individual sampling site and then, for each of the replicate clusters of three sites, extracting data from the LCS 88 for the amount of grassland, heather moorland and woodland within the area enclosed by all three circles (Fig. 2). In this way, we produced estimates of the relative amounts of each habitat type theoretically available to the deer which deposited faeces at the various sampling sites. It is well known that female red deer tend to keep within the same home range throughout the year, and data gathered with GPS tracking collars in the earlier study (Sibbald et al., unpublished data) showed that males occupied the same home range in late spring/early summer and in winter, dispersing over a larger area only for the period between early July and early November. We have no reason to believe that the red deer in this study had a significantly different pattern of

behaviour; therefore, differences in home range size are unlikely to be an issue for interpretation of the results.

#### Statistical analysis

We transformed proportions of the different forage types in the diet using the ArcSine transformation to normalise variances, and then analysed the transformed values from each faecal sample ( $n=96$ ) using Residual Maximum Likelihood (REML) analysis in Genstat (Lawes Agricultural Trust 2003), since the data were unbalanced. We declared disturbance level (disturbed and less disturbed) and habitat type (grassland, heather moorland and woodland) and their interactions as fixed effects. Wald statistics ( $W$ ), which use an asymptotic approximation of the chi-square distribution, were used to test for significance. We used individual faecal



**Fig. 2** Example diagram showing circles drawn around one of the replicate clusters of faecal collection sites in grassland (G), heather moorland (H) and woodland (W), each indicating a possible home range of approximately 970 ha. Estimates of land cover (LCS 88, MLURI 1993) within the area enclosed by the unbroken line were used to calculate the percentages of the main habitat types theoretically available to deer visiting the collection sites

sample values for the analysis, even though it was not possible to determine whether each sample came from a different animal. It is likely that most, if not all, of the samples were unique since only fresh material was used and groups of as many as 150 animals were observed moving through the study areas (Jayakody 2005). In each case, the *W* and *P* values quoted in the “Results” section are from the analysis of angular transformed data, but the estimated mean values were produced by back-transforming the data to proportions and converting to percentages.

**Results**

**Habitat availability estimates**

There was no significant difference between the estimated percentage cover of grassland theoretically available to deer

visiting the disturbed and less-disturbed sampling sites, although there was less heather moorland and less woodland in the disturbed areas than in the less-disturbed areas (Table 4). Peatland and water accounted for most of the remaining habitat in both disturbed and less-disturbed areas, with a relatively small percentage of montane vegetation in each (Table 4).

**Diet composition in spring**

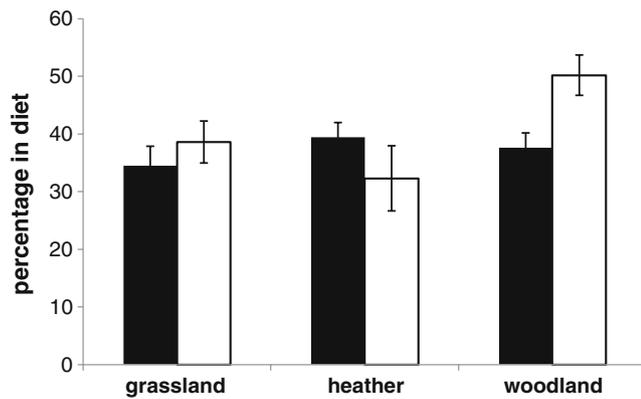
It was estimated that 39.2 (±1.38)% of the diet consisted of GSHR species, 57.9 (±1.33)% of heather, 1.7 (±0.30)% of berry and 1.2 (±0.25)% of tree species in spring. There tended to be less GSHR (37.0% vs 40.4%, *W*=3.17, *P*=0.08), more heather (59.8% vs 57.1%, *W*=2.90, *P*=0.09) and more tree (1.4% vs 0.4%, *W*=14.34, *P*<0.001) in the diet in disturbed than less-disturbed areas. There were no significant effects of the habitat type in which faeces were found on the percentage of GSHR, or heather in the diet, but there was a significantly higher percentage of berry in the diet of deer depositing faeces in grassland (3.0%) than heather moorland (2%) or woodland (0.6%) (*W*=21.47, *P*<0.001) and a significantly higher percentage of tree in the diet of deer depositing faeces in heather moorland (2.0%) than in grassland (0.6%) or woodland (0.2%) (*W*=57.58, *P*<0.001). There were significant interactions between effects of disturbance level and habitat type on the percentage of GSHR (*W*=6.46, *P*<0.05), heather (*W*=10.66, *P*<0.01) and tree (*W*=13.07, *P*<0.01) in the diet, with greater effects of disturbance on GSHR and heather indicated by faeces collected in woodland than grassland or heather moorland habitats (Figs. 3 and 4) and a greater effect of disturbance on the amount of tree in the diet in heather moorland (3.3% vs 0.5% for disturbed vs less-disturbed areas).

**Diet composition in winter**

In winter, only 13.8 (±0.90)% of the overall diet consisted of grass species, with 77.0 (±2.00)% heather, 8.4 (±1.46)%

**Table 4** Mean estimated percentage cover by six main habitat classes within a radius of 1,757 m around the faecal sampling sites in disturbed and less-disturbed areas

Habitat type	Disturbed	Less disturbed
Peatland	45.8	19.6
Heather moorland	26.4	40.0
Grassland	8.1	12.4
Coniferous woodland	4.4	17.7
Montane vegetation	7.8	4.6
Water	7.3	0



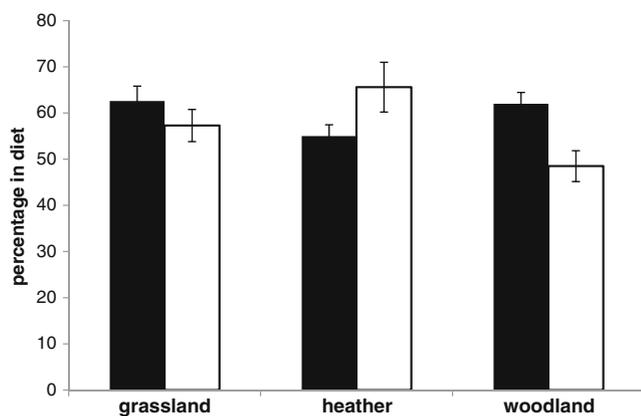
**Fig. 3** Mean percentage of GSHR (grass, sedges, herbs and rushes) in the diet of red deer in spring, estimated from faeces collected from disturbed (*black bars*) and less-disturbed (*white bars*) areas in grassland, heather moorland and woodland sites, with SE bars

berry and 0.8 ( $\pm 0.28$ )% tree. In contrast to spring, there was more grass ( $W=21.94$ ,  $P<0.001$ ), less heather ( $W=4.26$ ,  $P<0.05$ ) and less tree ( $W=6.84$ ,  $P<0.01$ ) in the diet in disturbed compared to less-disturbed areas (Fig. 5).

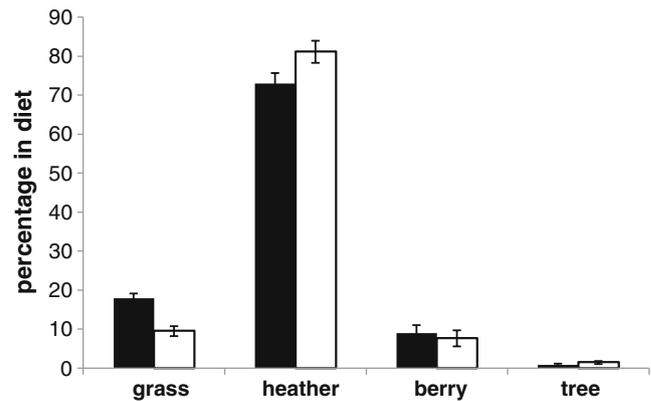
There were no effects of the habitat type in which the faeces were found on diet composition in winter, but the interaction between disturbance level and habitat type was significant for the grass species ( $W=8.08$ ,  $P<0.05$ ), with a greater effect of disturbance on the percentage of grass in the diet for faeces collected in woodland than the other habitats (Fig. 6).

## Discussion

We hypothesised that there would be a lower percentage of grass species in the diet of red deer in disturbed areas due to the exposed nature of open grassland. Since they need to

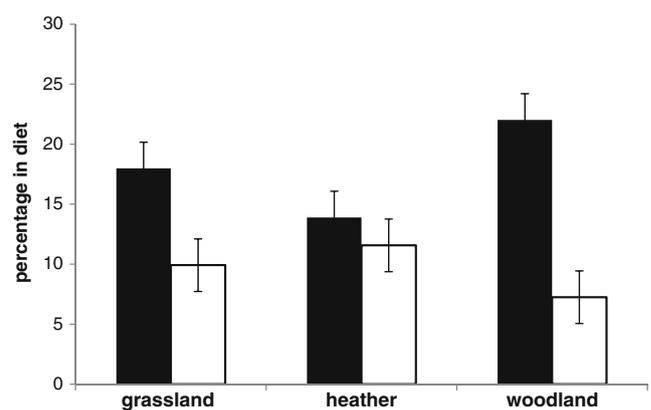


**Fig. 4** Mean percentage of heather in the diet of red deer in spring, estimated from faeces collected from disturbed (*black bars*) and less-disturbed (*white bars*) areas in grassland, heather moorland and woodland sites, with SE bars



**Fig. 5** Mean percentage of grass species, heather, berry and tree in winter, estimated from faeces collected from disturbed (*black bars*) and less-disturbed (*white bars*) areas, with SE bars

have their heads down to reach the vegetation, vigilance and feeding tend to be negatively correlated in grazing animals (Underwood 1982), and since red deer are generally more vigilant in grassland (Jayakody et al. 2008), foraging may be disturbed to a greater extent there than in other habitats. This hypothesis was supported by the spring results, but the effect was only significant for the faeces collected in woodland, although there was a tendency across all habitats. Our primary reason for collecting faeces from different habitat types was to avoid any bias from possible habitat effects. However, we did not expect habitat effects on diet composition, since the plant-derived material in faeces were just as likely to have come from some other habitat type as the one in which the faeces were found. Low-digestibility grass species and heather can take as long as 30 to 40 h to pass through the alimentary tract in deer (Milne et al. 1978) and deer can be expected to travel around 2 km per day in winter and as far as 5 km per day in late spring in that region (Sibbald et al. 2001), so that



**Fig. 6** Mean percentage of grass species in the diet of red deer in winter, estimated from faeces collected from disturbed (*black bars*) and less-disturbed (*white bars*) areas in winter in grassland, heather moorland and woodland sites, with SE bars

the likelihood of movement between habitat types within a day was fairly high. It is therefore not easy to explain the interactions between effects of disturbance and habitat type on diet composition.

In winter, by contrast, disturbance appeared to increase the amount of grass in the diet. However, the balance between recreation and hunting as sources of disturbance to red deer changes between summer and winter, with the winter months seeing both a reduction in the number of walkers using the tracks (Sibbald et al. 2011) and an increase in hunting activity (Bullock et al. 1999). Although the spatio-temporal nature of hunting activity is unpredictable, hunting is not normally carried out in areas that are frequently visited by the general public (i.e. those designated as ‘disturbed’ in this study) for reasons of safety. It is possible, therefore, that the lower percentage of grass in the diet in ‘less-disturbed’ areas in winter could have been due to increased vigilance by the deer in response to a higher incidence of hunting activity in these areas (Jayakody et al. 2008).

The feeding ecology of red deer has been studied extensively both under natural and farm conditions (e.g. Kay 1978; Fraser and Gordon 1997b; Latham et al. 1999), and it is well known that the appetite of red deer varies seasonally and that both sexes have a preference for grass over heather (e.g. Kay 1978; Milne et al. 1978; Clutton-Brock et al. 1982). In this study, the seasonal differences in overall diet composition, irrespective of disturbance level, accord with previous work showing that red deer tend to consume a diet with a higher proportion of grass in spring (Kay and Staines 1981; Staines et al. 1982; Latham et al. 1999). By winter, most perennial plants are in the dormant stage and there is a reduction in grass availability and biomass in the types of habitat found in the study area (Gordon 1989) so that the principal forage available to deer in winter is heather (Gimingham 2002b). The fact that the heather component of the diet increased to nearly 80% in winter in this study provides further evidence for the importance of temporal changes in availability for determining diet composition.

In spite of the methodological difficulties associated with studying free-ranging wild animals, such as the uncertain origin of the faecal material, we were able to detect differences in diet composition between disturbed and less-disturbed areas. We had to estimate habitat availability from aerial survey data, but our best estimates of percentage cover suggest that differences in availability were not biasing the results in spring. Although there was a much higher percentage cover of heather moorland in the less-disturbed areas, with no difference in grass cover, the deer in those areas tended to have more grass and less heather in their diet. However, in order to ensure that differences in diet composition were genuinely a result of disturbance, it would be necessary to control all the other factors affecting diet choice, which is not possible in a study of this type.

Clearly more research is needed to provide a definitive answer to the question of whether human disturbance in these areas has enough impact on diet composition to affect red deer performance, but we suggest that our study has provided some pointers to the way in which this question could be tackled. If disturbance does affect the amount of grass in the diet, it could be beneficial for the welfare of the animals to restrict public access in areas where deer traditionally feed in open grassland, at least during the peak growth period in spring when grassland species provide the best nutritional quality forage for red deer. Good nutritional status in the deer population is desirable for welfare reasons in areas used for recreation and also for economic reasons where hunting is a source of income. Control of disturbance levels close to preferred feeding grounds could be particularly beneficial for deer in montane areas where the availability of high-quality food is further restricted by a relatively short growing season (Birse and Dry 1970).

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