PROPOSING AN EFFICIENT INDICATOR OF GRAZER DISTRIBUTION ON HETEROGENEOUS HILL VEGETATION

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Abstract. Irish and UK uplands and peatlands are of international importance but are under threat from several factors, including heavy grazing pressure. Sheep preferentially graze patches of acid grassland with short dense swards, sometimes referred to as 'grazing lawns', and have been implicated in damage to uplands. The aim of this study was to increase our understanding of resource selection by grazers to further inform the design and implementation of conservation strategies. Grazing lawn frequency and habitat condition were mapped and GPS collars were used to track Scottish Blackface sheep on a hill farm in Ireland. Weighted compositional analysis (multivariate analysis of variance) was used to test for random use of different categories of grazing lawn frequency and habitat condition. Grazing lawn frequency was spatially uneven and habitat condition ranged from undamaged to very severely damaged areas. Typically, selection of differing categories of habitat condition was not significant ($P>0.05$), although the highest selection rank was consistently for the 'moderate-undamaged' category. Sheep most selected 1 ha grid squares containing numerous/extensive grazing lawns ($P<0.05$) day, night and year-round. As a simple, efficient indicator of hill use by sheep, which would be a valuable input in models predicting grazing impact on hill vegetation, the mapping of grazing lawn frequency is suggested.
Keywords: *agriculture; ecology; environment; resource management; resource selection*

Introduction

Irish and UK uplands and peatlands are of international importance due to the limited global distribution of the habitats, plant communities and fauna they support [9, 56]. Many of these habitats and associated species are protected under the EC Habitats (92/43/EEC) and Birds (79/409/EEC) Directives [21], and are included in biodiversity action plans [16, 37] and agri-environment scheme measures [14, 49]. Despite this, the quality of remaining upland and peatland continues to be under threat from heavy grazing pressure, burning, afforestation, peat extraction, undergrazing and/or land abandonment [22, 48, 56, 57].

Damage in this study refers to habitat conditions which fail to meet biological conservation objectives. While habitats are affected by natural phenomena such as topography [24] and wind-driven rain [11], management practices including grazing [55] play a key role in habitat condition and can be altered. Therefore, the focus of this study is on grazer behaviour as grazing is the predominant management practice on

Irish hills where heavy grazing pressure is a main threat [50]. This is also the case in other countries, particularly the UK [22, 48].

Damage assessment classifications have been devised for upland areas and include indicators of grazing-related damage [18, 44]. It is widely known that different grazing animals have different effects on vegetation and that different plant communities and associated soils have different carrying capacities [6, 29, 52]. Numerous researchers have studied the impacts of livestock grazing on upland systems (e.g. [8, 15, 23]) but it is believed that grazer selection of areas with differing condition status has yet to be quantified. It is known that sheep choose to use a small proportion of the total area available to them [61] and exhibit habitat and vegetation selection with a preference for acid grassland patches [12, 35, 61]. Acid grassland can have short, dense swards and often has abundant *Nardus stricta* (L.), [25] (characteristic plant species described). [45] referred to these conspicuous grassland patches as 'grazing lawns', probably because they are a product of grazing and resemble well maintained lawns.

Plant biomass and herbage intake rates are important factors in foraging efficiency and patch selection by grazers [12]. Damaged areas support a higher percentage cover of exposed soil and, consequently, a lower percentage cover of vegetation [18]. Conversely, grazing lawns have a dense canopy which promotes greater forage yields per bite compared with lightly grazed vegetation [45].

Surprisingly, very little published quantitative information is available on resource selection by sheep grazing heterogeneous hill vegetation [2]. Since then, valuable information on patch selection by sheep has been obtained using plot-based trials with artificial patches and field observations (e.g. [19, 28]), which complements previous trials by [12] for example. GPS tracking devices have recently been used to investigate habitat selection rankings in a complex hill farm environment by collecting a large amount of data round-the-clock with high location accuracy [61]. As management prescriptions on complex hill habitat assemblages probably need to vary between sites [35], GPS tracking, although useful for detailed studies on a number of sites, is unlikely to be carried out on a farm-to-farm basis. Therefore an alternative, more rapid method (that could be carried out at farm level) for estimating grazer distribution, to identify areas under greatest grazing pressure, would be a useful tool in conservation management. [61] investigated habitat selection rankings but acid grassland was considered to be under-represented and no account was taken of habitat condition. Therefore the objectives of this study are to investigate spatio-temporal use of grazing lawns (frequency classified for 1 ha grid squares) and patches with differing habitat condition status.

Methods

Study area

The study area comprised of 216.9 ha of upland and peatland at the Teagasc Hill Sheep Farm in Co. Mayo in the west of Ireland (53˚37' N, 09˚41' W). The dominant habitats were blanket bog and wet heath, with fragmented patches of acid grassland. Habitat distribution and sheep selection rankings of habitats are described in full by [61]. The study area, which was within the catchment area of the Erriff River, was part of the Mweelrea/Sheeffry/Erriff Complex candidate Special Area for Conservation and proposed Natural Heritage Area. The study area was on the south-southeasterly slopes of Ben Gorm and ranged in altitude from 15-275 m OD, with the highest, steepest slopes in the northwest corner. The site was Class 5 for agricultural land use [26]. Soils were mainly organic, consisting of peats, lithosols, humic/peaty podzols and gleys. Peat depths ranged between 30 and 525 cm [58]. Pegs marked a 100x100 m grid.

A maritime temperate climate prevailed with the nearest synoptic meteorological station located in Belmullet, Co. Mayo, approximately 70 km distant. Based on the most recent 30-year averages (1961-1990) recorded at Belmullet, the mean daily temperature was 14.0 °C in July and 5.7 °C in January, and the annual mean daily duration of bright sunshine was 3.5 h [46] undated. The mean annual rainfall 1993-2005 recorded on-site was 2086.4 mm (L. O'Malley *pers. comm.*). The minimum and maximum hours of daylight at the study area were calculated as 7 h 27 min and 17 h 4 min, respectively.

Scottish Blackface sheep grazed the study area at stocking rates of 0.4 ewes/ha in spring (March-May), 0.9 ewes/ha in summer (June-August) and autumn (September-November) and 0.8 ewes/ha in winter (December-February). These calculations were based on 2004-2005 averages, omitted lambs and included hoggets at a ratio of 3 hoggets:2 ewes. The land was grazed for 348 days in 2004 and 351 days in 2005 and supplementary feed was not given in the study area. Ewes lambed in early April with a productivity of 1.0 lamb/ewe (based on mean data 2004-2006). Approximately 80 females were retained annually as replacements. (L. O'Malley *pers. comm.*).

Tracking ewes

Four Scottish Blackface ewes ('core ewes') plus seven substitutes, all two years old, were selected at random at the start of the study. This age group was selected because it had experience of the study area and was likely to survive for the duration of the study. Substitute ewes were tracked only when core ewes were unavailable pre-lambing either because they were of low body condition or twin-bearing. Four ewes were tracked in each of nine season-based tracking periods between February 2004 and April 2006 producing 36 ranges in total. A 'range' is the collection of location data for an individual in any one tracking period. Simultaneous flock observations for 58% of ranges/64% of individuals [61] indicated no unusual social behaviour by collared ewes. However, one core ewe was a member of a social group that chose to occupy a fenced exclosure which was under a different grazing regime to that of the study area (removed from analyses as explained below).

GPS collars (GPS_2200R, Lotek Wireless, Ontario, Canada) weighing 720 g were used to track ewes. Collars were programmed to record locations at 10-min intervals using scheduling software (GPSHOST, Lotek Engineering, Ontario, Canada) and current satellite almanac files from Lotek. Locations were stored onboard the collar and retrieved after 5 weeks. This was the maximum time taken for recordings to cease, either through battery pack expiry or data storage capacity (5028 differential locations) being reached [43].

Location data were downloaded to a PC and corrected to increase accuracy using post-differential correction software (N4, V.1.2138, Lotek Engineering, Ontario, Canada) and files from the nearest active base station 54 km distant (NUI Galway Base Station, Ordnance Survey Ireland, www.osi.ie). Post-differentially corrected GPS data have an accuracy of approximately 7 m radius [41]. Locations with a position dilution of precision value of more than 10 were excluded to further increase accuracy without excessive loss of GPS data [13, 42].

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Habitat condition and grazing lawn frequency surveys

Habitat condition of the study area was originally mapped in 1999 [5] and ground-truthed for change in 2005. Assessment was made following the method described by [18] (now the National Parks and Wildlife Service) which uses six condition categories; undamaged, moderate-undamaged, moderately damaged, moderately-severely damaged, severely damaged and very severely damaged. These six categories are combined into three groups; undamaged, moderately damaged and severely damaged. Habitat condition indicators include but are not exclusive to grazing-related damage and are defined for each habitat type. Indicators include vegetation cover and growth, particularly the cover and condition of *Calluna vulgaris* (L.) Huds and the cover of *Nardus stricta* (L.), species richness, sward height, exposed soil and evidence of burning.

Grazing lawn frequencies were allocated for each complete or part 100x100 m grid square in 2005. Categories of grazing lawn patches (~4-7 m^2 or the equivalent area) were; (i) none, (ii) few (1-5 patches), (iii) several (6-10) and (iv) numerous/extensive (>10). In the instance of a part grid square, on the boundary of the study area, it was classified as numerous/extensive if acid grassland occupied ≥0.3 of its area.

The habitat condition and grazing lawn frequency maps were digitised using geographical information system software (ArcGIS Desktop, V.9.1, ESRI Inc., Redlands, CA, USA).

Data analysis

Data handling

Typically in wildlife tracking studies, animals are caught, tagged and released within their home range. However in this study, the flock was brought in from the study area, collars were fitted to selected ewes in an adjacent yard and then sheep were released from the yard and left to make their own way back to their chosen areas. To explore habitats selected by sheep and filter out data directly influenced by handling, the first 3 days after release were excluded. This 3-day period was chosen objectively by identifying core areas as 95% cores from inflections on cluster polygon incremental analysis plots [40] and scrutinising location data against 95% polygons to identify the time taken for sheep to leave the yard, reach a 95% polygon and stay there for longer than an overnight stop en route (taken as 11 h 51 min, the annual mean non-daylight hours). The longest time taken by an individual was 2 days 23 h, rounded to 3 days.

Spatial and temporal autocorrelation of GPS data

Locations from the same individual are not independent data, therefore tests for resource selection were based on summary statistics of resource use from the individual [38, 39] using compositional analysis. This allows comparison of both multiple individuals and resource categories in the same test [1]. Of the 36 ranges from nine tracking periods, 11 individuals were tracked and consequently 11 ranges (one per individual) were potentially suitable for compositional analysis. Range selection was made objectively, regardless of season, based on Minimum Convex Polygon (MCP) incremental analysis which is indicative of range stability [39], i.e. ranges where ewes were most settled were selected. Two individuals were omitted because; (a) dynamic interaction analyses [39] showed only two of 11 ranges were non-independent (Jacob's index was 0.769 based on geometric mean distances between same-time locations) so only one range (the most stable) of the pair was used and (b) one individual chose to occupy a fenced exclosure outside the study area that was under a different management regime, affecting resource classification. The final sample size was nine because (a) data that breach analysis assumptions of data independence or misrepresent typical habitat availability to the flock were rigorously omitted and (b) the cost of the tracking collars and replacement battery packs for each sampling period was a limiting factor. Sample sizes for seasonal tests differ and are explained below.

Ranges of individuals tracked in more than one season were suitable for separate seasonal tests. However, ranges were also included in seasonal analyses where the same individual was tracked for the same season for more than one sampling year. This may breach test assumptions of data independence but these ranges are included to minimise omission of data as independence could not be tested. Six of the original 36 ranges were omitted because the same individual repeatedly occupied an area outside the study area, and two further ranges were omitted as dynamic interaction analyses indicated that data (from three pairs of ranges consisting of three individuals and three ranges) were not independent (Jacob's index >0.5). Therefore, 28 ranges were suitable for seasonal tests.

Datasets

Seven datasets were produced in this study (*Table 1*). The 'Complete' dataset contained all post-processed data for the nine independent ewes. This dataset was then subdivided to form two additional datasets, 'Diurnal' and 'Nocturnal', based on mean sunrise and sunset times for each range. Seasonal datasets were produced that contained all post-processed data, excluding three days post-release, for 28 ranges divided between the four seasons.

Table 1. *Composition of datasets*

Dataset	No. of ranges	No. of individuals	No. of years sampled	Total no. of locations
Complete	9	9	3	21 250
Diurnal	9	9	3	11 073
Nocturnal	9	9	3	10 177
Spring	9	8	3	14 353
Summer	7	4	2	20 967
Autumn	6	3	2	17 359
Winter	6	3	2	15 070

Range and resource analysis

The tracked ewe location data, habitat condition map and grazing lawn frequency map were imported into range analysis software (Ranges7, Anatrack Ltd, Dorset, UK). MCPs were produced which link the outermost locations and are widely used as a broad estimate of animal ranges (e.g. [1]). The boundary of the study area, i.e. the area available to animals, was determined by a stockproof fence in this instance. Habitat condition and grazing lawn frequency analyses were performed using Ranges7 to estimate (i) the resource content of the study area, (ii) resource content of ranges (i.e. MCPs) and (iii) resource use at location.

Statistical analysis

Selection of habitat condition and grazing lawn frequency categories was examined using weighted compositional analysis (Compos Analysis V.6.2+, Smith Ecology Ltd, Abergavenny, UK). Proportions of resource use were compared with those available, using Wilks' lambda (Λ) test (MANOVA). Analyses were carried out at two selection levels based on selection levels identified by [36]:

(i) broad, comparing proportions of resources present within ewe ranges with those available in the study area accessible to sheep, and

(ii) detailed, comparing proportions of resources used at location with those available within individual ewe ranges.

It is unlikely that resource use and available percentage data follow a multivariate normal distribution, hence randomisation tests were used to evaluate the significance of Λ and t values [1].

Results

Ewe locations

Most occupation during day, night and year-round was in the northwest quarter of the study area (*Figs 1, 2*). Nocturnal locations were distinctly more clustered than diurnal locations (*Fig. 1b, c*). While seasonal distribution patterns could not be compared in this instance because the individuals tracked and number of individuals and ranges differ (*Table 1*), *Figure 2* indicates a tendency towards seasonal variation.

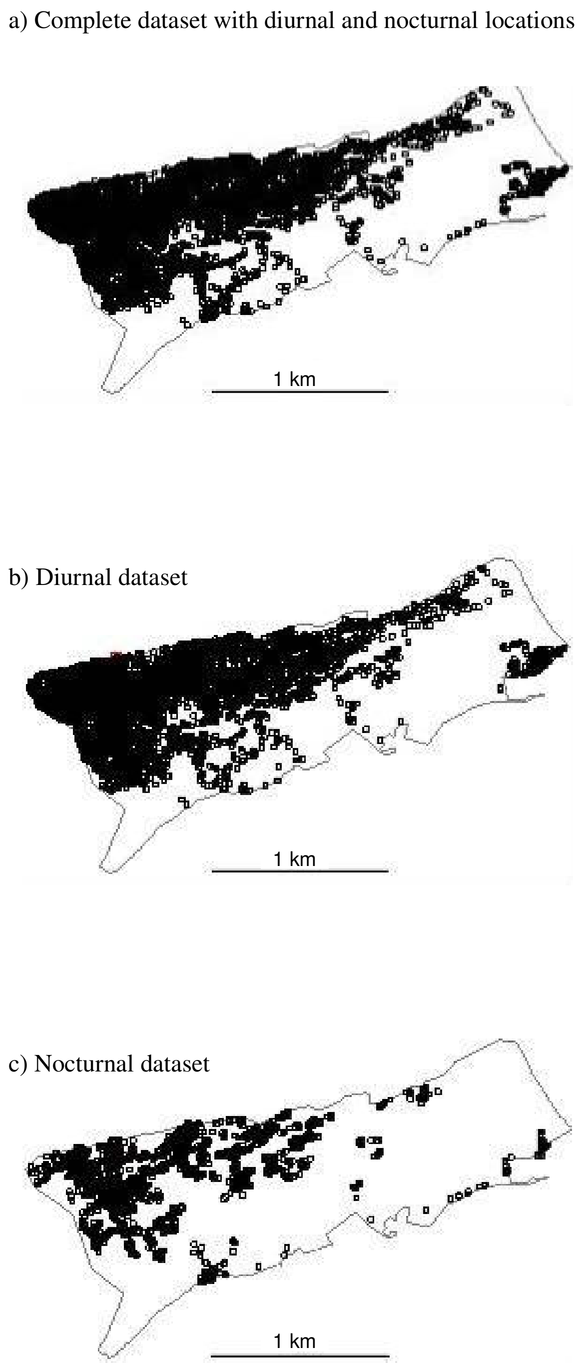

Figure 1. *Location data of nine ewes tracked between February 2004 and April 2006 using GPS collars.*

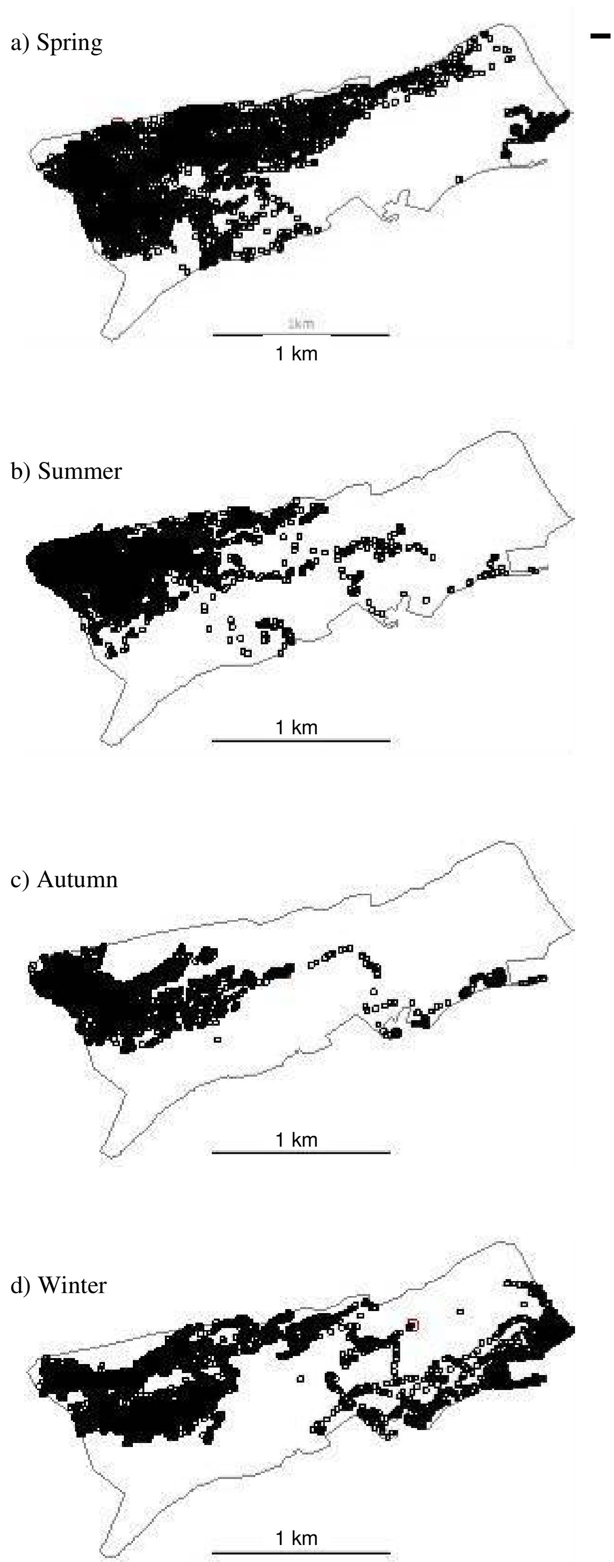

Figure 2. *Seasonal location data of ewes tracked between February 2004 and April 2006 using GPS collars.*

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Grazing lawn frequency

The dominant categories of grazing lawn frequency available across the study area were few (36.8%) and numerous/extensive (34.3%), (*Table 2a*). Distribution of grazing lawns was clearly uneven with the most numerous/extensive occurring in the northwest corner (*Fig. 3*). Use was significantly non-random (P<0.05) with numerous/extensive patches consistently selected most at broad and detailed selection levels, day and night, and across all four seasons (*Table 3*). There was slight variation in sequences of the subsequent three ranks between broad and detailed selection levels (*Table 3*), day and night (*Table 3a, b*), summer and the other three seasons at the broad level (*Table 3c*), and between autumn and the other three seasons at the detailed level (*Table 3d*). ‘None’ was consistently selected least at the broad level for all seven datasets (*Table 3a, c*) but mostly this was not the case at the detailed level (*Table 3b, d*).

Table 2. *Availability of grazing lawns and habitat conditions in the 216.9 ha study area.*

Category	% available	Group
a) Grazing lawn frequency		
None	11.4	n/a
Few (0-5)	36.8	n/a
Several (6-10)	17.4	n/a
Numerous (>10)/extensive	34.3	n/a
b) Habitat conditions		
Undamaged (U)	29.5	Undamaged (U)
Moderate-undamaged (MU)	22.3	Moderately damaged (M)
Moderately damaged (M)	21.0	Moderately damaged (M)
Moderate-severely damaged (MS)	5.5	Moderately damaged (M)
Severely damaged (S)	2.0	Severely damaged (S)
Very severely damaged (VS)	19.8	Severely damaged (S)

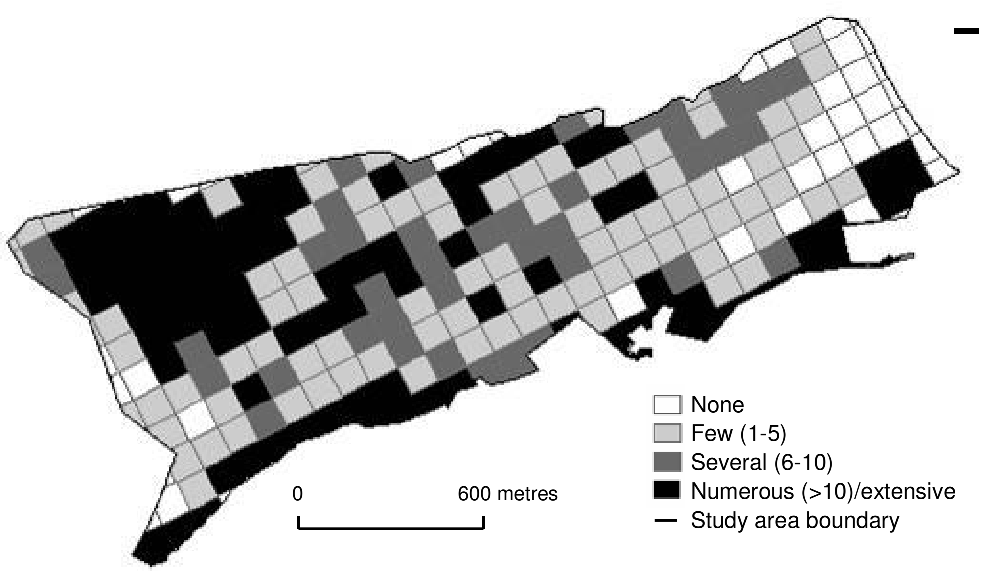

Figure 3. *Distribution of grazing lawns by grid square.*

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Table 3. *Tests for random use, by Scottish Blackface hill sheep, of grid squares consisting of varying grazing lawn frequencies. The grazing lawn frequency ranking is shown in parentheses when Λ is not significant and '>>>' denotes a significant difference between two consecutively ranked frequency categories.*

Dataset	Randomness test Λ	P	Grazing lawn frequency rankings (most>least selected)	% of total locations
a) Nine individuals, broad selection level (MCP[a] vs. study area)				
Complete	0.293	0.015 *	Numerous >>> several > few >>> none	100.0
Diurnal	0.270	0.005 **	Numerous >>> several > few >>> none	100.0
Nocturnal	0.280	0.003 **	Numerous >>> few > several > none	100.0
b) Nine individuals, detailed selection level (locations vs. MCP)				
Complete	0.111	0.005 **	Numerous > none > several > few	100.0
Diurnal	0.138	0.027 *	Numerous > none > several > few	100.0
Nocturnal	0.187	0.006 **	Numerous >>> several > none > few	100.0
c) Seasonal use, broad selection level (MCP vs. study area)				
Spring	0.237	0.006 **	Numerous >>> few > several >>> none	100.0
Summer	0.021	0.042 *	Numerous >>> several > few >>> none	100.0
Autumn	0.189	0.127	(Numerous > few > several >>> none)	100.0
Winter	0.362	0.285	(Numerous > few > several >>> none)	100.0
d) Seasonal use, detailed selection level (locations vs. MCP)				
Spring	0.149	0.036 *	Numerous > none > several > few	100.0
Summer	0.185	0.116	(Numerous > none > several > few)	100.0
Autumn	0.059	0.026 *	Numerous > several > few > none	100.0
Winter	0.151	0.185	(Numerous > none > several > few)	100.0

Habitat condition

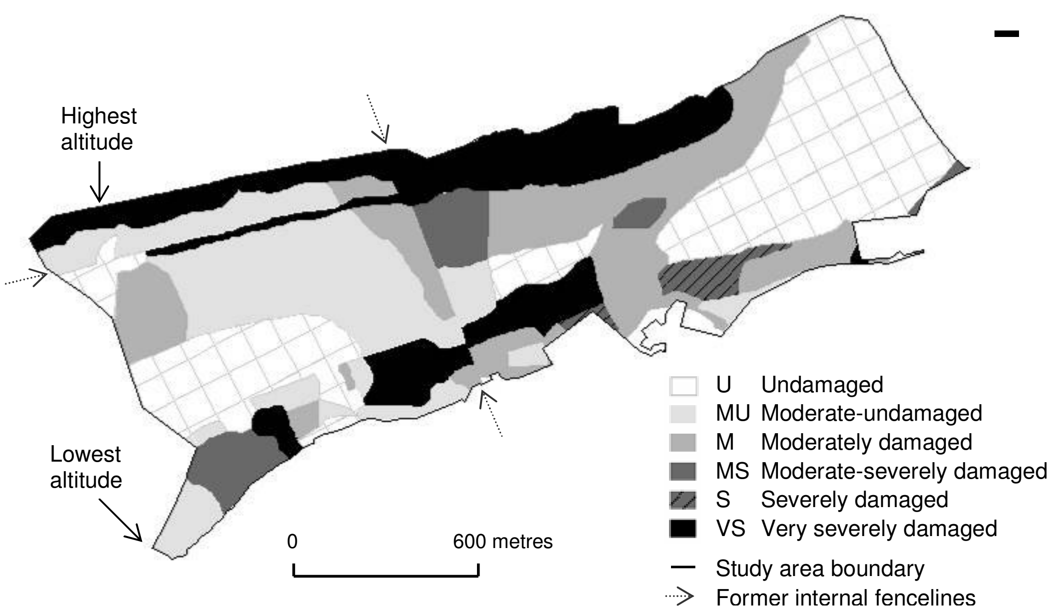

Figure 4. *Habitat condition map of the study area.*

All six categories of habitat condition, from undamaged to very severely damaged, occurred across the study area (*Table 2b, Fig. 4*). The most severe damage was associated mainly with blanket bog on the mountain ridge (northern boundary) and also, in places, at low altitude (*Fig. 4*). Two former internal fencelines were evident on the habitat condition map. An initial visual comparison between the sheep occupation and habitat condition figures suggested that the most abundant habitat condition in the northwest quarter of the study area, where sheep occupation tended to be concentrated, was moderately damaged.

Use of habitat condition categories was random for 20 of 28 tests which suggests that selection by ewes was not significant ($P>0.05$), (*Table 4, 5*). Nevertheless, rank sequences are still thought to be meaningful [61]. The moderate-undamaged category was consistently selected most at the broad and detailed levels, day and night, and across all seasons with the exception of autumn at the detailed level where it was the second-most selected category (*Table 4a, b; Table 5a, b*). Very severely damaged areas were second-most selected with nine ewes at the broad level and in summer at both levels (*Table 4a; Table 5a, b*), selected least for the remaining three seasons at the detailed level (*Table 5b*), of intermediate ranks at the detailed level with nine ewes (*Table 4b*) and of various ranks for seasons at the broad level (*Table 5a*). Undamaged areas were selected considerably more within ewe ranges by day than at night when they were selected least (*Table 4b*).

Table 4. *Tests for random use of habitat condition categories by nine individual Scottish Blackface hill sheep based on three datasets. The habitat condition ranking is shown in parentheses when Λ is not significant and '>>>' denotes a significant difference between two consecutively ranked condition categories.*

Dataset	**Randomness test** Λ	*P*	**Habitat condition rankings (most>least selected)**[a]	**% of total locations**
a) Broad selection level (MCP[b] vs. study area) with all six categories				
Complete	0.266	0.172	(MU > VS > M > MS > U > S)	100.0
Diurnal	0.156	0.033 *	MU > VS > M > MS > U > S	100.0
Nocturnal	0.217	0.120	(MU > VS > M > MS > S > U)	100.0
b) Detailed selection level (locations vs. MCP) with all six categories				
Complete	0.000	0.065	(MU > M > VS > U > MS > S)	100.0
Diurnal	0.005	0.023 *	MU > U > M > VS > MS > S	100.0
Nocturnal	0.000	0.032 *	MU > M > VS > MS > U > S	100.0
c) Broad selection level (MCP[b] vs. study area) with three condition groups				
Complete	0.535	0.104	(M>S>>>U)	100.0
Diurnal	0.547	0.114	(M>S>>>U)	100.0
Nocturnal	0.391	0.045 *	M>S>>>U	100.0
d) Detailed selection level (locations vs. MCP) with three condition groups				
Complete	0.312	0.030 *	M>S>U	100.0
Diurnal	0.456	0.105	(M>U>S)	100.0
Nocturnal	0.650	0.672	(M>U>S)	100.0

[a]U = Undamaged area, MU = Moderate-Undamaged area, M = Moderately damaged area, MS = Moderate-Severely damaged area, S = Severely damaged area, VS = Very Severely damaged area.
[b]MCP = Minimum Convex Polygon, used to estimate ewe ranges.

Severely damaged and moderate-severely damaged categories were omitted from seasonal analyses at the detailed level (*Table 5b*) because low use prohibited analyses

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from running, hence tests were repeated with data for all six categories combined into three condition groups (*Table 2*). Consistent with findings using six categories where moderate-undamaged was generally most selected, the moderately damaged group was selected most at both selection levels, day, night and year-round except in summer at the broad selection level when severely damaged areas were most selected (*Table 4c, d; Table 5c, d*).

Table 5. *Seasonal tests for random use of habitat condition categories by Scottish Blackface hill sheep. The habitat condition ranking is shown in parentheses when Λ is not significant and '>>>' denotes a significant difference between two consecutively ranked condition categories.*

Dataset	**Randomness test Λ**	***P***	**Habitat condition rankings (most>least selected)[a]**	**% of total locations**
a) Broad selection level (MCP[b] vs. study area) with all six categories				
Spring	0.105	0.066	(MU > M > VS > U > MS > S)	100.0
Summer	0.004	0.067	(MU > VS >>> U > M > S > MS)	100.0
Autumn	0.000	0.031 *	MU >>> U > M > VS > S >>> MS	100.0
Winter	0.047	0.318	(MU > M >>> U > MS > VS > S)	100.0
b) Detailed selection level (locations vs. MCP) with all six categories				
Spring	0.296	0.179	(MU > M > U > VS)	100.0
Summer	0.255	0.164	(MU > VS > M > U)	100.0
Autumn	0.198	0.283	(U > MU > M > VS)	100.0
Winter	0.434	0.448	(MU > M > U > VS)	100.0
c) Broad selection level (MCP vs. study area) with three condition groups				
Spring	0.431	0.013 *	M>>>S>U	100.0
Summer	0.404	0.095	(S>M>>>U)	100.0
Autumn	0.244	0.082	(M>>>U>S)	100.0
Winter	0.442	0.028 *	M>U>S	100.0
d) Detailed selection level (locations vs. MCP) with three condition groups				
Spring	0.346	0.151	(M>U>S)	100.0
Summer	0.565	0.286	(M>S>U)	100.0
Autumn	0.198	0.070	(M>U>S)	100.0
Winter	0.304	0.168	(M>U>S)	100.0

[a]U = Undamaged area, MU = Moderate-Undamaged area, M = Moderately damaged area, MS = Moderate-Severely damaged area, S = Severely damaged area, VS = Very Severely damaged area.
[b]MCP = Minimum Convex Polygon, used to estimate ewe ranges.

Discussion

Sheep distribution

Sheep occupation being concentrated in the northwest quarter of the study area is probably attributable directly and indirectly to topography with the highest elevation, steep slopes, shelter-providing bowl-like features, shallower and better-drained soils and the most extensive patches of relatively better forage quality and availability than elsewhere in the area [4, 17, 57, 61].

Nocturnal GPS location data were more clustered than diurnal locations which was expected as sheep are well known to be active mostly during daylight hours and to rest at night [20, 59, 61]. Whilst sheep of other breeds have been reported to usually congregate in the same places at night [3], Scottish Blackface individuals do not return

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to the same place every night [31]. This is consistent with this study's findings of multiple nocturnal rest sites for nine tracked individuals (*Fig. 1c*). This probably does not have implications for management because, although occupying different nocturnal rest sites implies dispersal was greater than if sheep returned to the same sites, individuals have been found to occupy just 9-20% of this study area [61].

Grazing lawn frequency

Grid squares with numerous/extensive grazing lawns were associated with a range of features, i.e. a large bowl-like feature and adjacent hillock in the northwest corner, the riverbank on the western half of the southern boundary, farm tracks and earth banks along the eastern half of the southern boundary, and scattered hillocks, rock outcrops and/or sloping ground with relatively well-drained soils. Absence of grazing lawns was typically associated with areas of waterlogged, deep, quaking peat on relatively level ground, and occasionally with very steep north-facing slopes inaccessible to sheep on the northern boundary.

The most extensive grazing lawns were found in the northwest of the study area which correlates with sheep occupation patterns. Numerous/extensive patches were consistently selected most, probably because acid grassland habitats are preferred most by sheep on hills [12, 60, 61] and are a product of heavy grazing [25, 45].

Sheep most selected grid squares containing numerous/extensive grazing lawns even in winter which is inconsistent with possible expectations from reviewing literature as resources on favoured patches deplete after the growing season [35] and grazing lawns on this study site were previously found to be dominated by *Molinia caerulea* [51] which dies back in early autumn. Selection in winter of grid squares with numerous/extensive grazing lawns is probably explained by Scottish Blackface sheep being known to return to home ranges that are learned from dams [32] and to graze in close proximity to grassland patches [12]. Sheep were probably utilising alternative habitats as grid squares that contained numerous/extensive grazing lawns usually supported and may have been dominated by different habitats, particularly wet heath.

Habitat condition

Wind-driven rain and its effect on soil erosion is reported to be most severe close to the top of a hill [11], and this probably contributed to much of the damage associated with the mountain ridge along the northern boundary of the study site. The thin strip of severely damaged habitats running parallel to this in the northwest quarter marked a former fenceline (that was removed in 2001) along which poaching and sheep paths were observed, where sheep traversed the hill between shelter-providing bowl-like features dominated by acid grassland. Two severely damaged compartments on the southern boundary were associated with deep peat, relatively level ground, waterlogging most of the year, former peat extraction in places and routes habitually taken when sheep were gathered and released from the yard.

Grazers can facilitate damage to upland habitats, conversely, they increase diversity in plant species composition and structure and the fauna this supports [55]. For this reason, and because habitat condition assessment took flora diversity into account, the northwest area most occupied by sheep was predominantly classified as undamaged to moderately damaged. While increasing diversity has ecological benefits, acid grassland patches replace wet heath [27, 56, 57] which, unlike acid grassland, is listed under

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Annex I of the Habitats Directive. Some acid grassland is desirable but the spread of grassland patches is likely and poses a threat to heathland communities [12].

Use of areas with differing categories of habitat condition was mostly random, which indicates there was not a direct correlation between sheep occupation and habitat condition. This is partly attributable to other factors of erosion that are not grazing-related and partly because the carrying capacity of different plant communities and topography vary. It is speculated that the main reasons are diet selection as discussed below and that the mapping accuracy of vegetation condition (following the guidelines) is much lower than that of the GPS location data. Additionally, a limitation of this study is that it is based on detailed information from only a small number of individuals, causing low power in statistical tests. However, this study justifies further research with larger sample sizes.

Findings that support possible expectations that use of damaged areas by sheep would be low include the selection ranking being lowest for very severely damaged areas in all seasons except summer and highest for moderate-undamaged areas in all seasons. Conversely, very severely damaged areas had the second-highest selection rank in several tests, and most tests for habitat condition selection were not significant ($P>0.05$), suggesting that sheep did not avoid damaged areas.

Very severely damaged areas had the second-highest selection rank in summer at both selection levels and the severely damaged condition group was most selected at the broad selection level in summer. This is consistent with the notion that hill sheep like the 'bare bite', i.e. sheep graze bare areas despite the availability of lush vegetation patches. This could be explained by selective grazing for preferred species during the growing season as [30] reported high proportions of *Narthecium ossifragum* (L.) Huds and *Eriophorum spp.* (L.) in the diets of Scottish Blackface sheep grazing blanket bog, and these species were dominant on areas of exposed peat (i.e. severely damaged areas) in this study.

Implications for conservation

Based on the finding that sheep consistently selected grid squares containing numerous/extensive grazing lawns, an efficient indicator of hill use by sheep would be to map acid grassland frequency following the simple method introduced in this study. This could have a secondary purpose of identifying areas of wet or dry heath most at risk of grazing-related damage, as most heather damage is known to occur within 5 m of grassland patch edges [12]. Grazing lawns contribute to the biodiversity value of a site [53] but are a threat to heathland communities that have been identified as being more important for conservation [21]. Determining correct stock numbers and management practices are crucial to prevent an increase in the number or extent of grazing lawns and to meet conservation objectives. Limits of acceptable change should be set for the proportion of grazing lawns and the extent of grazing lawns should be monitored.

The full spectrum of habitat conditions from undamaged to very severely damaged areas occurring on one site, combined with uneven use by grazers with unlimited access, supports the widely held belief that a single stocking rate for upland and peatland sites is inadequate. Stocking rate calculations need to be based on relative proportions of habitats available and habitat condition, as recognised by [49], and habitat selection exhibited by grazers [61]. In light of grazer distribution not corresponding directly to habitat conditions, stocking rates calculated at site level are probably still not enough to arrest and reverse grazing-related damage because areas of different categories of habitat condition require different action.

Various recommendations have been made to arrest damage to vegetation and promote recovery. A reduction in sheep numbers is often recommended [3, 7, 34]. Additional recommendations include sheep exclusion from severely damaged areas until vegetation has recovered [8, 54], cutting thrice-yearly of undamaged, but arguably undergrazed, *Molinia caerulea* (L.) Moench-dominant areas to promote recovery by *Calluna vulgaris* (L.) Hull [47] and mixed grazing of cattle or goats with sheep [10, 33]. However, cutting would not be a practical option on a site such as that studied with deep peats and steep slopes prohibiting tractor access, and grazing cattle would need to be restricted to periods when water levels are low to minimise poaching by heavier animals. Benefits from allowing vegetation to recover would include improved ecological, landscape and livestock production quality.

To conclude, a comprehensive understanding of resource use by grazers is fundamental in designing conservation strategies and management planning should consider habitat condition and grazer distribution as previously recognised. This study presents an efficient method for realising this objective, based on hill sheep selection of grid squares containing higher frequencies of grazing lawns. Use of very severely damaged areas was greatest in summer during the plant growing season and therefore inhibiting vegetation recovery. Temporary exclusion of livestock or reducing stocking rates during this season would facilitate an improvement in habitat condition. However, management recommendations cannot be inferred beyond the study area without further research on a number of sampling sites and with different habitat condition assemblages. The methods presented, including the rapid mapping of grazing lawn frequency introduced in this study and easily collecting vast, accurate data using GPS devices, are recommended for use in such studies in the future.

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