

RESOURCE SELECTION BY HILL SHEEP: DIRECT FLOCK OBSERVATIONS VERSUS GPS TRACKING

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Abstract. Uplands and peatlands are of international ecological importance and heavy grazing pressure has been implicated in a decline in their condition. Therefore, a better understanding of grazer behaviour could aid the design of conservation strategies. The objective of this study was to test whether the same resource selection results were obtained from direct flock observations as simultaneously-run GPS tracking studies. Direct flock observations were conducted on 50 sampling days, June 2004-July 2005. Habitat, habitat condition and grazing lawn frequency maps were produced. Resource use and availability were estimated using range analysis and GIS, and resource selection was analysed using weighted compositional analysis. Flock distribution was uneven with a mean of 0.0-8.9 sheep/ha observed based on a 1 ha grid system. Habitat selection based on direct observations varied seasonally with acid grassland-related habitats selected most in spring, summer and autumn, and wet heath and blanket bog selected most in winter. Moderately damaged areas and grid squares containing numerous/extensive grazing lawns were consistently selected most ($P < 0.05$). Resource selection findings based on direct flock observations were consistent with those obtained using detailed GPS tracking data from fewer individuals. Resource management recommendations are discussed.

Keywords: *agriculture; ecology; environment; resource management; resource selection*

Introduction

Uplands and peatlands are of international importance for their associated flora and fauna and restricted global distribution and extent. Associated habitats, such as ‘temperate Atlantic wet heath with *Erica ciliaris* and *Erica tetralix*’ and active ‘blanket bog’, are recognised as priority habitats for conservation at a European level (European Commission, 2008). Heather-dominated landscapes are reported to be best represented in the British Isles (Thompson *et al.*, 1995b), which also supports 18-22% of the world’s blanket bog (Cadbury, 1987, Department of Arts Heritage Gaeltacht and the Islands, 2002). However, grazing-related damage to European uplands is most notable

in the UK and Ireland (European Environmental Advisory Councils, 1999) where sheep farming is the prevalent land use. This damage is probably attributable to relatively high sheep numbers; of nearly 26 million breeding sheep in northern Europe, 80% are on the British Isles (Dýrmundsson, 2006).

EU policy has a large influence on the management of areas with poor soil and climatic conditions for agricultural production, such as upland areas. Irish sheep farmers (mainly hill sheep farmers, L. Connolly *pers. comm.*) are highly dependent on direct payments and additional subsidies, for example, excluding subsidies, production costs exceeded incomes generated in 2006 (Connolly *et al.*, 2007). EU policy in recent decades encouraged high stock numbers which resulted in grazing-related damage (Gillmor and Walsh, 1993), conversely, there is now increasing concern that changes in financial support will lead to undergrazing and land abandonment in European uplands (Moravec and Zemeckis, 2007). Grazing animals are widely recognised as an important management tool in ecological conservation (Rowell and Clarke, 1988, Thompson *et al.*, 1995a) and agri-environment schemes provide support to hill farmers that is essential if grazers are to be kept on upland areas. A better understanding of grazer behaviour could increase the efficacy of agri-environment schemes.

Provenza and Cincotta (1993) recognised the difficulty in predicting foraging behaviour. A complex computer-based hill grazing management model of sheep stocking regime impacts on hill vegetation has been developed (Armstrong *et al.*, 1997a; Armstrong *et al.*, 1997b). This model has been used by various organisations to aid decision-making (Hester and Baillie, 1998) and a new version of this model, which incorporates additional components, is awaiting further data for validation before release (HillPlan; Macaulay Institute, 2009).

Grazer preferences have been investigated using analysis of faecal, stomach and oesophageal samples (Heady, 1964; Williams, 1969; McInnis *et al.*, 1983). Seasonal diet selection of hill sheep has been reported in several studies (Welch, 1984; Bullock, 1985; Grant *et al.*, 1985, Grant *et al.*, 1987). Vibracorders, sensors built into GPS collars and video recordings have been used to investigate sheep behaviour including activity, circadian rhythm and inter-animal distances (Hulbert *et al.*, 1998; Iason *et al.*, 1999; Sibbald *et al.*, 2000; Umstätter *et al.*, 2008). Direct observations of hill sheep behaviour activity, location and orientation have also been made (Hunter, 1962; Berggren-Thomas and Hohenboken, 1986; Clarke *et al.*, 1995; Hester *et al.*, 1999).

Scottish Blackface is the dominant hill sheep breed in the British Isles and, therefore, the obvious choice as the study animal. Informative studies of habitat selection by hill sheep have previously been based on direct observation data at the very detailed plant community level (Hunter, 1962) or within 2.5 ha plots and with only two habitats available (Clarke *et al.*, 1995). The former has practical limitations for large-scale repeatability and the latter excludes a number of habitats typically available on heterogeneous hill areas.

Key findings from studies by the same authors, which used GPS tracking collars on hill sheep with access to a mosaic of upland and peatland habitats, are that sheep; (i) occupied only 9-20% of the area available to them, (ii) selected acid grassland most and avoided blanket bog, (iii) mostly selected 1 ha grid squares that contained numerous/extensive grazing lawns (patches of grassland with short, dense swards that have been heavily grazed (McNaughton, 1984) and (iv) did not avoid severely damaged areas with comparatively low forage availability (Williams, 2008; Williams *et al.*, 2009).

The objectives of this study are (i) to investigate resource selection based on direct flock observations and (ii) to compare these results (that have a relatively large sample size) with findings from GPS tracking collars on a limited number of sheep (Williams, 2008; Williams *et al.*, 2009) which were made at the same time. The implications for conservation strategies using the two methods are also discussed.

Methods

Study area

The study area consisted of 216.9 ha of upland and peatland at the Teagasc Hill Sheep Farm in Co. Mayo, Ireland (53°37'N, 09°41'W). The dominant habitats were blanket bog and wet heath, with fragmented patches of acid grassland. The study area was within the catchment area of the Erriff River and part of the Mweelrea/Sheeffry/Erriff Complex candidate Special Area for Conservation and proposed Natural Heritage Area. The general aspect was south-southeasterly and the altitude ranged from 15-275 m OD, with the highest, steepest slopes in the northwest corner of the study area. The site was Class 5 for agricultural land use (Gardiner and Radford, 1980). Soils were mainly peats and peat depths ranged between 30 and 525 cm (Walsh *et al.*, 2000).

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 (Met Éireann, *undated*). The mean annual rainfall recorded on-site (1993-2005) 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.

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 study area was grazed for 348 days in 2004 and 351 days in 2005. 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.*). Sheep had open access across the site, which was marked with pegs in a 100 × 100 m (1 ha) grid.

Direct flock observations

Sheep locations and behaviour activities were recorded for individuals at the time of sighting. Locations were estimated to the nearest grid square and behaviour activity categories used followed those of (Hester *et al.*, 1999), i.e. grazing, moving, standing, lying, interacting and other ('other' activities included defecating, scratching against a post and the shaking of rain water from fleeces).

Flock observations were made from along a set route, approximately 8.2 km in length, designed (i) to minimise disturbance to sheep before recording locations and behaviour activities and (ii) to gain sight over most of the study area. Flock observations began at 10:00 local time and took approximately 5 hours to complete. Recordings were made in all weather conditions using a Dictaphone sealed in a ziplock plastic bag and

transcribed to an Excel spreadsheet. Flock observations were conducted twice weekly for five weeks for each of five seasonal sampling periods between June 2004 and July 2005, providing a total of 50 sampling days.

Habitat, habitat condition and grazing lawn frequency surveys

Habitats were mapped using the UK and Irish classifications and guidelines (Nature Conservancy Council, 1990; Fossitt, 2000; Heritage Council, 2002) to enable comparison with other studies, increased replicability and further applications. Habitat patches ≥ 0.25 ha were mapped with the aid of colour, ortho-corrected aerial photographs taken in 2000 (Ordnance Survey Ireland, Dublin, Ireland). Habitats are referred to throughout by the Irish classification names, the UK equivalents are detailed in Williams (2008).

Habitat condition of the study area was originally mapped in (Bleasdale and Heffron, 1999) and ground-truthed for change in 2005. Assessment was made following the method described by Dúchas the Heritage Service and the Department of Agriculture and Food (1999) which uses six condition categories; undamaged, moderate-undamaged, moderately damaged, moderately-severely damaged, severely damaged and very severely damaged. Habitat condition indicators include (but are not exclusive to) grazing-related damage, are defined for each habitat type, and 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.

All acid grassland patches were grazing lawns, a product of intensive grazing, but acid grassland patches were under-represented on the habitat map because patches were fragmented and often too small to map following mapping guidelines. To efficiently obtain more information on acid grassland distribution, grazing lawn frequency by grid square was mapped. Grazing lawn frequencies were allocated for each full or part 100×100 m grid square in 2005. Categories of grazing lawn patches ($\sim 4\text{--}7\text{ m}^2$ 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, habitat condition and grazing lawn frequency maps were digitised using Geographical Information System (GIS) software (ArcGIS Desktop, V.9.1 & 8.3, ESRI, Redlands, CA, USA).

Data analysis

Resource analysis

The habitat, habitat condition and grazing lawn frequency maps were imported into range analysis software (Ranges7, Anatrack Ltd, Dorset, UK) and analyses performed to estimate resource content of the study area. Availability and flock use of these resources based on grid squares was estimated using ArcGIS (including the identity tool) and Excel (including pivot tables).

Statistical analysis

During the daily 5 hour direct flock observations, visibility conditions (high or low) were recorded. Spearman's rank correlation test (implemented using SPSS v.15, Chicago, Illinois, USA www.spss.com) was used to test whether there was a correlation between visibility conditions and the proportion of the flock sighted.

Selection of habitat, habitat condition and grazing lawn frequency categories was examined using weighted compositional analysis (Compos Analysis V.6.2+, Smith Ecology Ltd, Abergavenny, UK). Each sampling day was weighted by the number of observations. Proportions of resource use were compared with those available, using Wilks' lambda (Λ) test (MANOVA). (Aebischer et al., 1993) used a two-step approach based on Johnson's selection levels (Johnson, 1980), which was previously implemented with the GPS data, comparing (i) habitats available within the study area with those used within ewe ranges (broad level) and (ii) habitats available within ewe ranges compared with those used at location (detailed level), (Williams, 2008). This method was repeated with GPS data for habitat condition and grazing lawn frequency (Williams *et al.*, 2009). However, with the flock observation data, only a one-step approach could be used, comparing resources available within the study area with those used at the 1 ha grid square level. This estimate is intermediate between the broad and detailed levels because there is no precise location data and most individuals were unmarked prohibiting ewe range estimates.

Compositional analysis tests are based on percentage values, which overcame the potential problem arising from the inclusion of part and complete grid squares. Resource use and available percentage data will not have an exact multivariate normal distribution, and hence randomisation tests were used to evaluate the significance of Λ and t values (Aebischer *et al.*, 1993).

All sampling days were combined for annual tests, with summer resource use and number of observation values averaged because this season was duplicated. To enable comparison with results previously obtained from a limited number of sheep tracked using GPS simultaneous to these direct flock observations, tests were repeated using three habitat and three habitat condition groups (*Table 1a,c*). Where the two combination habitats (characteristics of two habitats were exhibited in these instances, i.e. blanket bog-acid grassland and wet heath-acid grassland) overlapped two habitat groups, values were divided equally between the two corresponding habitat groups.

A total of 8791 sheep observations were made over the 50 sampling days. All were suitable for analysis of sheep behaviour activities and proportions of the flock sighted. Sixty-five observations were omitted from compositional analyses as these were of sheep that chose to occupy a fenced enclosure outside the study area and were unsuitable for resource selection analysis because different management practices in the enclosure affected classification of habitats, habitat condition and grazing lawn frequency.

Table 1. Availability of habitats, grid squares containing different frequencies of grazing lawns and areas of differing habitat condition in the 216.9 ha study area

Category	Abbreviated name/code	Area (%)	Group
a) Habitat			
Blanket bog	Blanket bog	52.8	Bog
Wet heath	Wet heath	35.3	Heath
Semi-natural dry-humid acid grassland	Acid grassland	3.0	Grassland
Wet heath-Semi-natural dry-humid acid gsld	Heath-grassland	2.4	Heath & grassland
Cutover bog	Cutover bog	2.0	Bog
Dense bracken	Bracken	1.6	Grassland
Blanket bog-Semi-natural dry-humid acid gsld	Bog-grassland	1.6	Bog & grassland
Eroding blanket bog	Eroding bog	0.5	Bog
Semi-natural wet grassland	Wet grassland	0.5	Grassland
Buildings and artificial surfaces	Track	0.4	Grassland
Earth banks	Earth banks	0.1	Grassland
b) Grazing lawn frequency			
None	None	11.4	N/A
Few (0-5)	Few	36.8	N/A
Several (6-10 or equivalent)	Several	17.4	N/A
Numerous (≥ 10)/extensive	Numerous	34.3	N/A
c) Habitat condition			
Undamaged areas	U	29.5	Undamaged (U)
Moderate-undamaged areas	MU	22.3	Moderately damaged (M)
Moderately damaged areas	M	21.0	Moderately damaged (M)
Moderate-severely damaged areas	MS	5.5	Moderately damaged (M)
Severely damaged areas	S	2.0	Severely damaged (S)
Very severely damaged areas	VS	19.8	Severely damaged (S)

Results

Direct flock observations

A mean of 79.1 % (min. 57.6 %, max. 94.6 %) of the flock was sighted on 50 sampling days. The Spearman rank test indicated that the proportion of the flock sighted was not affected by visibility conditions (correlation coefficient=0.168, $P=0.245$, $n=50$).

Grazing was the main behaviour activity observed with means of 63.1-94.6 % of sightings per sampling period (*Fig. 1*). Lying was the second-most observed activity with means of 2.5-30.2 % of sightings per sampling period. Proportions of sheep sighted grazing were highest in winter. The highest proportions of sheep sighted lying were in both summers and autumn. The number of observations was low in spring because ewes were taken off the study area and given supplementary feed prelambling if twin-bearing or of low body condition.

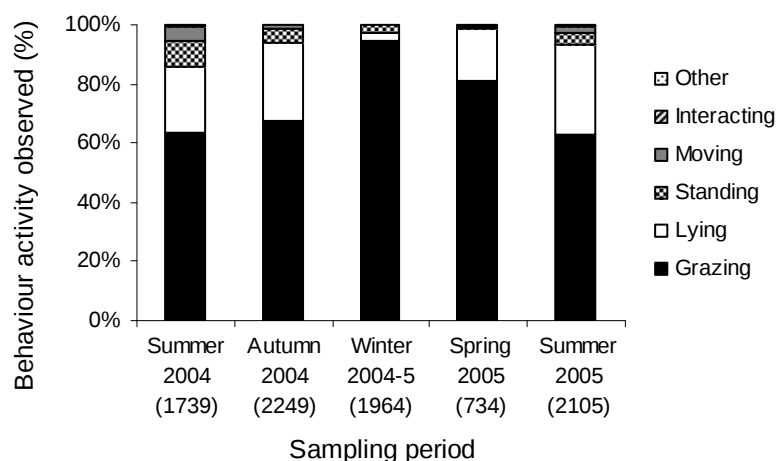


Figure 1. Mean proportions of behaviour activities of Scottish Blackface hill sheep observed on 10 days for each of five seasonal sampling periods. The total number of sheep observations made in each sampling period is included in x-axis labels

Flock distribution across the study area was clearly uneven (Fig. 2). Five categories, with four manual breaks in sheep density values, were used to identify (i) unoccupied grid squares (0.00), (ii) squares occupied at or below densities expected based on the annual stocking rate of 0.74-0.75 ewes/ha (L. O'Malley *pers. comm.*), (iii) squares occupied at densities greater than expected based on the annual stocking rate (>0.75 , subdivided into two categories using the mean midpoint between 0.75 and the highest mean observed density). Sheep densities were lower overall in spring as most of the flock was brought in for supplementary feed prelamming. Sheep densities were higher overall in summer as sheep numbers observed included hoggets and lambs whereas annual stocking rate calculations excluded lambs and included hoggets as ewes at a 3:2 ratio (L. O'Malley *pers. comm.*). A preference for the northwest quarter of the study area was most marked in summer (2004 and 2005) compared with alternative seasons. Between season and year variation was evident in flock distribution, although distribution was most similar for the two consecutive summers sampled.

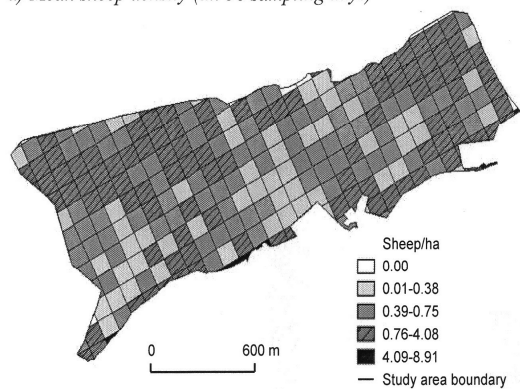
The mean sheep density by grid square across all 50 sampling days indicated a preference for the northwest quarter and northeast corner of the study area (Fig. 3a). Mean densities per sampling period and overall are presented in Figures 2 and 3a but absolute sheep densities by grid square for the 50 sampling days found observed densities ranged between 0.00 and 158.13 sheep/ha with a mean density of 0.93 sheep/ha. However, the highest observed sheep density for each sampling period was consistently found in part grid squares on the boundary of the study area ranging in size between 0.05 and 0.13 ha. The highest number of sheep seen in a grid square at any one time was 23 and this occurred in complete, 1 ha grid squares on two occasions (i.e. a density of 23.00 sheep/ha).

On any one sampling day, sheep were observed to be dispersed across the study area, as opposed to being congregated in one group. Frequency histograms indicated that typically the majority of grid squares were unoccupied, none were occupied at low densities between 0.01 and 0.93 sheep/ha, and sheep occupation was at densities of ≥ 0.94 sheep/ha (Fig. 4).

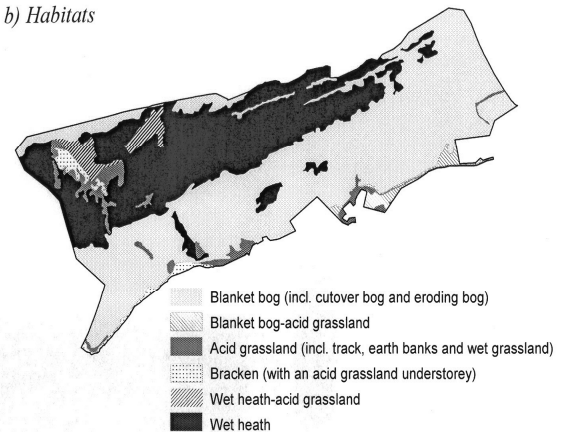


Figure 2. Mean sheep density by grid square from 10 days for each of five seasonal sampling period

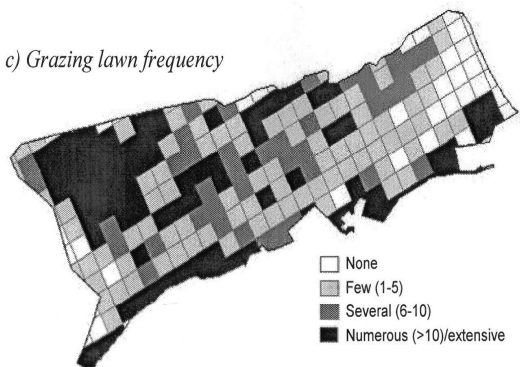
a) Mean sheep density (all 50 sampling days)



b) Habitats



c) Grazing lawn frequency



d) Habitat condition

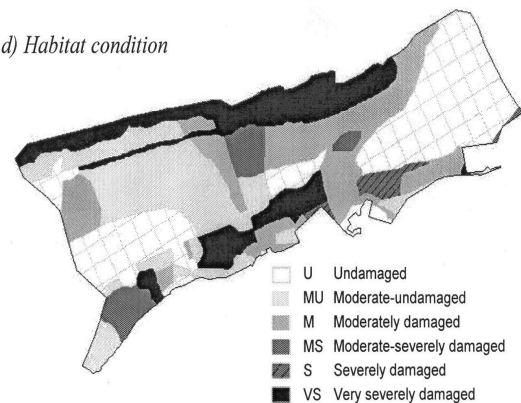


Figure 3. Spatial distribution maps of sheep occupation, habitats, grazing lawn frequencies and habitat conditions for the study area.

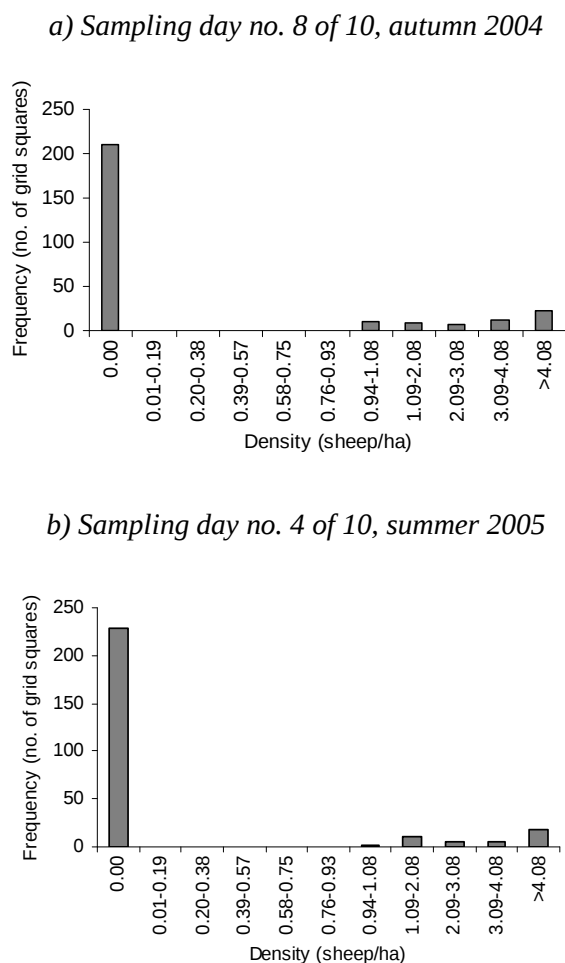


Figure 4. Sheep densities observed in the study area which consisted of 270 grid squares. These are typical frequency histograms from two randomly-selected sampling days.

Data presented in sub-sections are based solely on direct flock observations.

Habitat selection

Eleven polygon habitats were available to grazers (*Table 1a*). The dominant habitats were blanket bog and wet heath, which combined accounted for 88.1% of the study area (*Table 1a*, *Fig. 3b*). Wet heath was mostly associated with the slopes of the northern half of the study area and blanket bog with the more level areas, typically at lower altitudes.

Table 2. Tests for random use of habitats by Scottish Blackface hill sheep based on direct observations. The habitat ranking is shown in parentheses when Δ is not significant and '>>>' denotes a significant difference between two consecutively ranked habitats.

Sampling period(s)	Randomness test	Habitat rankings (most>least selected)	No. of sheep sightings	% of total sightings
a) Tests with nine habitats				
Annual 2004-5	0.308 ≤0.001***	Bracken>Acid grassland>Track>Bog-grassland>Wet heath>>>>Blanket bog>Heath-grassland>Cutover bog>Wet grassland	8692	99.6
Summer 2004	0.101 0.324	(Bracken>Acid grassland>Heath-grassland>Track>Wet heath>Bog-grassland>Blanket bog>Cutover bog>Wet grassland)	1728	99.5
Autumn 2004	0.010 0.040 *	Acid grassland>Track>Heath-grassland>Bracken>Cutover bog>Bog-grassland>Wet heath>Blanket bog>Wet grassland	2223	99.9
Winter 2004-5	0.192 0.558	(Wet heath>>>>Blanket bog>Track>Bracken>Acid grassland>Heath-grassland>Bog-grassland>Cutover bog>Wet grassland)	1954	99.8
Spring 2005	0.047 0.178	(Bracken>Track>Bog-grassland>Acid grassland>Wet heath>Blanket bog>Heath-grassland>Wet grassland>Cutover bog)	721	99.3
Summer 2005	0.023 0.073	(Bracken>Heath-grassland>Acid grassland>Bog-grassland>Track>Wet grassland>Cutover bog>Wet heath>Blanket bog)	2066	99.3
b) Tests with three habitat groups				
Annual 2004-5	0.519 ≤0.001***	Grassland>>>>Heath>>>>Bog	8726	100.0
Summer 2004	0.251 0.019 *	Grassland>>>>Heath>>>>Bog	1737	100.0
Autumn 2004	0.520 0.086	(Grassland>>>>Heath>Bog)	2226	100.0
Winter 2004-5	0.463 0.021 *	Grassland>Heath>>>>Bog	1957	100.0
Spring 2005	0.200 0.003 **	Grassland>>>>Heath>Bog	726	100.0
Summer 2005	0.109 0.002 **	Grassland>>>>Heath>Bog	2080	100.0

Habitat selection tests (*Table 2a*) were conducted with only nine of the 11 polygon habitats because earth banks and eroding bog had to be omitted since too many zero values, indicative of low use, prohibited analyses running. Habitat selection by sheep was only significant ($P < 0.05$) for autumn and annual tests, although habitat ranks were still considered to be meaningful (Williams, 2008). Bracken (*Pteridium aquilinum* L. Kuhn) was selected most in both summers and spring, and acid grassland was selected most in autumn. Wet heath followed by blanket bog were most selected in winter whereas these two habitats were of intermediate to low rank in the other seasons. No two rank sequences were identical, indicating variation between seasons and years.

To include all polygon habitat data and to simplify comparison with results previously obtained from GPS tracking of ewes (section 3.5), the 11 habitats were combined into three groups (*Table 1a*) and tests re-run. Habitat group selection was significant ($P < 0.05$) for all tests except autumn (*Table 2b*). The selection rank for all tests was consistently acid grassland-related habitats selected most, followed by wet heath, and blanket bog habitats selected least.

Grazing lawn frequency selection

Grid squares containing few (36.8 %) and numerous/extensive (34.3 %) grazing lawns were the most frequently occurring (*Table 1b*). The largest block of grid squares containing numerous/extensive grazing lawns was found in the northwest corner of the study area, some were also located along the southern boundary and scattered elsewhere (*Fig. 3c*).

Selection of grid squares containing different frequencies of grazing lawns was significant ($P < 0.05$) annually and for all seasons except winter (*Table 3*). All four categories were suitable for analysis and did not lend themselves to further grouping as with habitat selection analyses. Grid squares containing numerous/extensive grazing lawns were selected most overall and in all seasons tested. The rank of the subsequent three categories varied slightly between seasons and years.

Table 3. Tests for random use, by Scottish Blackface hill sheep, of grid squares consisting of varying grazing lawn frequencies (based on direct observations). 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.

Sampling period(s)	Randomness test		Grazing lawn frequency rankings (most>least selected)	No. of sightings	% of total sightings
	Λ	P			
Annual 2004-5	0.459	≤ 0.001 ***	Numerous>>>Several>None>Few	8726	100.0
Summer 2004	0.135	0.008 **	Numerous>None>Several>Few	1737	100.0
Autumn 2004	0.304	0.035 *	Numerous>None>Several>Few	2226	100.0
Winter 2004-5	0.908	0.877	(Numerous>None>Several>Few)	1957	100.0
Spring 2005	0.144	0.013 *	Numerous>>>Several>>>Few>None	726	100.0
Summer 2005	0.069	0.002 **	Numerous>>>Several>None>Few	2080	100.0

Habitat condition selection

All condition categories from undamaged to very severely damaged areas occurred in the study area (*Table 1c*). The most dominant single category available was undamaged areas (29.5 %). Moderately damaged categories combined accounted for 48.8 % of the study area and severely damaged categories combined accounted for 21.8 %. A mosaic of habitat conditions was found (*Fig. 3d*). Severely damaged areas were most associated with the mountain ridge and, in places, at low altitudes. Moderate damage was mostly associated with the northern half of the study area and undamaged areas were mostly associated with more level areas at low altitude.

Selection of areas with varying habitat condition, using all six categories, was significant ($P < 0.05$) annually and for all seasons except winter (*Table 4a*). Moderate-undamaged areas were selected most in both summers, autumn, spring and annually but second-least in winter when moderately damaged areas were selected most. Severely damaged areas were selected least in all tests except second-least in summer 2005. Very severely damaged areas had a low selection rank of five out of six in autumn, rose to four in spring, and were selected more in summer of both years and spring with a selection rank of three.

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

Sampling period(s)	Randomness test		Habitat condition rankings (most>least selected) ^a	No. of sightings	% of total sightings
	Λ	P			
a) Tests with six condition categories					
Annual 2004-5	0.446	$\leq 0.001^{***}$	MU>M>U>>>VS>MS>>>S	8726	100.0
Summer 2004	0.169	0.036 *	MU>>>M>VS>U>MS>S	1737	100.0
Autumn 2004	0.036	$\leq 0.001^{***}$	MU>U>M>MS>VS>S	2226	100.0
Winter 2004-5	0.154	0.053	(M>U>VS>MS>MU>S)	1957	100.0
Spring 2005	0.085	0.011 *	MU>>>M>U>VS>MS>S	726	100.0
Summer 2005	0.134	0.039 *	MU>M>VS>U>S>MS	2080	100.0
b) Tests with three condition groups					
Annual 2004-5	0.341	$\leq 0.001^{***}$	M>>>U>>>S	8726	100.0
Summer 2004	0.710	0.223	(M>S>U)	1737	100.0
Autumn 2004	0.047	0.003 **	M>U>>>S	2226	100.0
Winter 2004-5	0.365	0.017 *	M>U>S	1957	100.0
Spring 2005	0.218	0.006 **	M>>>U>>>S	726	100.0
Summer 2005	0.444	0.040 *	M>>>S>U	2080	100.0

^aU = undamaged, MU = moderate-undamaged, M = moderately damaged, MS = moderate-severely damaged, S = severely damaged, VS = very severely damaged areas.

The six condition categories were grouped into the three broader categories (*Table 1c*) defined by Dúchas the Heritage Service and the Department of Agriculture and Food (1999) and selection tests were re-run. Selection was significant ($P < 0.05$) annually and for all sampling periods except summer 2004 (*Table 4b*). Moderately damaged areas were consistently selected most in all tests. Severely damaged areas were selected least annually and in autumn, winter and spring, whereas severely damaged areas were second-most selected in both summers.

While visual comparison of the four maps presented in *Figure 3* suggests there is not a clear, direct link between flock distribution, habitats, grazing lawn frequencies and/or habitat condition, in summary, compositional analysis results suggest that flock distribution was generally associated with acid grassland, numerous/extensive grazing lawns and moderately damaged areas.

Direct flock observations and GPS tracking results compared

Habitat rank sequences with three habitat groups based on direct flock observations matched those based on GPS data for all seasons at the detailed selection level and for summer and autumn at the broad level. When comparing flock observations with GPS data at the broad level with five habitats common to both sets of tests, there were similarities and differences. Examples of similarities include wet heath being selected most in winter and acid grassland selected most in autumn with blanket bog least, preceded by wet heath in both sets of results. Examples of inconsistencies in results between methods include blanket bog selected second-most in winter with flock observations but least with GPS data, and bracken selected most in spring with flock observations but second-least with GPS data.

Grid squares containing numerous/extensive grazing lawns were most selected in all tests, i.e. in all seasons and at all selection levels, based on direct flock observations and GPS tracking data (Williams *et al.*, 2009).

Moderately damaged areas were consistently selected most in tests using flock observation data and GPS data (Williams *et al.*, 2009). Both methods indicated a higher selection of severely damaged areas in summer (results from GPS data presented in (Williams *et al.*, 2009), although this was also found to be true in spring using flock observation data.

Discussion

Direct flock observations

The majority of the flock was sighted when following the chosen route. Complex topography with hummocks, hollows and steep slopes obscured some sheep from view and hindered observer access to some areas. Visibility did not affect proportions of the flock sighted.

Grazing was the main behaviour activity observed and more so in winter than other seasons, which is consistent with findings by others. Scottish Blackface sheep are reported to graze hill vegetation 79% of daylight time in winter (Hulbert *et al.*, 1998), 53% in summer (Clarke *et al.*, 1995) and 60% in summer and autumn (Hester *et al.*, 1999). Proportions of sightings are probably indicative of time spent on respective behaviour activities and values for summer and autumn are similar to those of (Hester *et al.*, 1999). Feeding blocks were available in the trial by (Hulbert *et al.*, 1998) which may

explain the lower proportion of time spent grazing in winter compared with observations in this study where no supplementary feed was available.

Uneven sheep distribution and a preference for the northwest quarter of the study area are consistent with findings from GPS data (Williams, 2008) and are likely to be explained by resource selection as discussed below. Hill sheep, including Scottish Blackface, are thought to learn home ranges from their dams and are known to return to the same areas (Hunter and Milner, 1963; Lawrence and Wood-Gush, 1988). Foraging behaviour is also reported to be influenced by experiences of individuals (Provenza and Cincotta, 1993). Therefore, a feedback loop probably occurs between experience gained of environmental conditions, including habitats, grazing lawns and habitat condition, and home ranges subsequently passed on to offspring/learned. High occupation of the northwest quarter of the study area is consistent with findings that hill sheep prefer the area with the highest elevation (Berggren-Thomas and Hohenboken, 1986).

A striking finding is that sheep densities ranged between 0.00 and 158.13 sheep/ha (0.00-8.91 mean over 50 sampling days). Many studies of hill sheep behaviour are plot-based trials which provide valuable information but cannot explore sheep densities applicable to open hill situations. Conversely, Lawrence and Wood-Gush (1988) studied sheep behaviour on an open hill area but did not report on sheep densities. Hewson and Wilson (1979) reported a maximum of 35 sheep and 14 lambs on a heavily grazed coastal grassland area about 1.6 ha in size (equivalent to 30.6 sheep/ha). A comparison between Hewson and Wilson's study and the present study would be unfair because different methods were used, including the use of a 1 ha grid and more advanced technology (i.e. GIS software) in this study. Occasional highs of 16 sheep in 0.1 ha (equivalent to 158.1 sheep/ha but strongly influenced by grid positioning) and 23 sheep in complete, 1 ha grid squares (i.e. equivalent to 23.0 sheep/ha) were observed in this study. This information highlights the level of selection that can be exhibited by hill sheep on heterogeneous upland topography and associated vegetation.

The highest observed sheep density (158.13 sheep/ha) occurred in mid-October 2004 when the weather was dry, windy and overcast with high visibility. Sixteen sheep were observed occupying a grid square which was on the mid-northern boundary and only 0.10 ha in size, estimated using ArcGIS. The grid square was on the mountain ridge, with steep slopes and rock outcrops indicative of shallower soils than elsewhere, and dominated by wet heath.

Habitat selection

In tests with nine habitats, bracken was most selected in both summers and spring, probably because it supported an understorey of acid grassland, and acid grassland was selected most in autumn. Acid grassland-related habitats were consistently selected most in tests with three habitat groups. Preference for grassland on heterogeneous hill vegetation is consistent with findings by others (Welch, 1984; Clarke *et al.*, 1995; Hester *et al.*, 1999). Probable explanations for a preference of acid grassland include high vegetation productivity potential (McNaughton, 1984), higher protein and energy concentration and plant biomass (Doyle, 1979, Doyle, 1982) and higher digestibility and herbage intake on acid grassland than heath or blanket bog (Hodgson *et al.*, 1991).

Seasonal variation in habitat rankings based on nine habitats is probably explained by seasonal variation reported in plant palatability and hill sheep diets (Bullock, 1985, Grant *et al.*, 1987). For example, acid grassland patches in the study area are dominated by *Molinia caerulea* (L.) Moench (O'Dowd, 2005) which dies back in early autumn and

this provides a likely explanation for the top selection rank of wet heath as opposed to acid grassland in winter. When habitats were grouped, the broad selection trends were found but detail at habitat level was lost which is probably why heath was second to grassland-related habitats in winter for this test. This highlights the importance of conducting analyses with separate habitats (and ensuring sample sizes are large enough to do so) in addition to habitat groups because wet heath and blanket bog habitats were most selected in winter, which has important management implications.

Blanket bog-related habitats were consistently selected least, or most 'avoided', in tests based on the three habitat groups. Likely explanations include low vegetation productivity, digestibility and herbage intake, and a deficiency in minerals (Hodgson *et al.*, 1991), combined with taller vegetation which sheep find more difficult to graze (Grant *et al.*, 1985). Additionally, features associated with this habitat that made it difficult for sheep to move through, included bog pools, surface water, drainage ditches and areas of quaking peat.

Minor variation in habitat selection rank sequences between tests based on direct flock observations and GPS tracking data may be explained by flock observation analyses being intermediate between broad and detailed selection levels tested with GPS data. However, trends were generally consistent and led to the same conclusions.

Grazing lawn frequency selection

Grid squares containing numerous/extensive grazing lawns were associated with 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 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 distribution of grazing lawns is probably explained by sheep being reported to congregate and produce grazing lawns where vegetation productivity potential is high and to disperse from areas where potential is low (McNaughton, 1984).

Sheep most selected grid squares containing numerous/extensive grazing lawns in all seasons, which is consistent with findings based on GPS data (Williams *et al.*, 2009). A close association between flock and grazing lawn distribution was expected as grazing lawns are a product of intensive grazing. During the plant growing season, selection is probably explained by the relatively better forage quality and availability of acid grassland as discussed above. Selection for grid squares containing numerous/extensive grazing lawns outside the vegetation growing season, when forage quality of acid grassland is relatively lower, is probably explained by sheep known to return to learned home ranges and to concentrate grazing activity in close proximity to grassland patches rather than further away (Clarke *et al.*, 1995; Hester and Baillie, 1998). Additionally, grid squares typically supported and were often dominated by alternative habitats such as wet heath.

Habitat condition selection

Severely damaged areas were most associated with the mountain ridge, which is probably largely explained by wind-driven rain and its effect on soil erosion reported to be most severe close to the top of a hill (Choi, 2002). Severely damaged areas on the

southern boundary at low altitude were associated with deep peat, relatively level ground, waterlogging most of the year, former peat extraction in places and poaching on routes used when sheep were gathered and released from the yard. Moderately damaged areas were mostly associated with steeper slopes dominated by wet heath where sheep paths traversed the hill. Undamaged areas were species poor, dominated by tall, rank purple moor-grass and were arguably undergrazed.

Grazers can facilitate damage to upland habitats, conversely, they increase diversity in plant species composition, height and structure and the fauna this supports (Rowell and Clarke, 1988). While increasing diversity has benefits, creation of acid grassland patches is at the expense of wet heath (van Eck *et al.*, 1984; Gillmor and Walsh, 1993; Thompson *et al.*, 1995b) which, unlike acid grassland, is listed under Annex I of the Habitats Directive. Some acid grassland patches are inevitable where livestock graze hill vegetation and the spread of grassland patches is likely (Clarke *et al.*, 1995).

Moderately damaged areas were selected most, which was consistent with GPS data. Relatively better forage quality associated with these areas, compared with severely damaged areas that support higher proportions of exposed soil and undamaged areas that support tall vegetation that is difficult to graze, provides a probable explanation.

Higher selection of severely damaged areas in summer is consistent with findings from GPS data (Williams *et al.*, 2009), although this study also found this to be true in spring. Use of severely damaged areas particularly during the vegetation growing season raises concerns as grazing-related pressure is likely to inhibit recovery in areas where the proportion of exposed peat is highest. Seasonal selective grazing for preferred species probably explains use of these areas as Scottish Blackface sheep are thought to be more selective in summer when environmental heterogeneity is highest (Lawrence and Wood-Gush, 1988). *Eriophorum spp.* (L.) and *Narthecium ossifragum* (L.) Huds) were abundant species on areas of exposed peat and (Grant *et al.*, 1987) reported high proportions of these in the diets of Scottish Blackface sheep grazing blanket bog during the plant growing season.

Implications for conservation

An important finding from this study based on direct flock observations was that habitat, grazing lawn frequency and habitat condition selection trends matched those previously obtained from thousands of GPS tracking data for only a small number of individuals. This adds credence to findings from these two, very different research methods, indicating that both methods produced results that are likely to be representative of the flock. Additionally, it reinforces management recommendations previously made (including by Williams (2008) and Williams *et al.* (2009)). These recommendations were that; (i) stocking rate calculations should be based on grazer behaviour, relative proportions of habitats available and habitat condition, (ii) areas of habitats selected least (i.e. avoided; blanket bog habitats in this study) should be omitted from stocking rate calculations, (iii) additional measures, such as fencing, are probably also necessary to meet conservation objectives, (iv) stocking rates should not increase the number or extent of acid grassland patches at the expense of heathland, (v) grazing lawn frequency mapping could be used as an indicator of grazer distribution and subsequent grazer impact predictions, and (vi) additional information on grazer selection should be gathered and incorporated into hill management models such as HillPlan (Macaulay Institute, 2009) and used to aid decision-making.

Flock distribution ranged between grid squares that were unvisited and where very high stocking densities were observed on occasion. Uneven grazing pressure combined with all six habitat conditions occurring in the one study area, which was managed as a single unit, makes management planning problematic. Areas with different condition categories and carrying capacities require different management prescriptions but compartmentalising an upland/open hill site, e.g. using fencing, is labour intensive and expensive, neither of which are conducive to the hill sheep enterprise with high dependence on off-farm employment and low profit margins (Connolly *et al.*, 2007). Exclusion of grazers from targeted areas and sheep numbers calculated based on habitat availability, grazer selection and habitat condition, should facilitate vegetation recovery on exposed peat and reduce grazer impact on damaged areas. In this and similar instances, grazers should be excluded from extensive severely damaged areas, e.g. the area associated with the mountain ridge, and effects monitored. Gathering sheep is an essential practice for production and animal welfare and routes that cross blanket bog were unavoidable, therefore use of erosion control mats or other ground reinforcement technology to withstand and contain trampling pressure on localised eroded patches could be considered.

Seasonal selection rankings of habitats, grazing lawns and habitat conditions provide useful information that could be used to predict foraging behaviour and consequently grazer impact on vegetation. Seasonal grazing regimes should be devised that meet habitat conservation objectives at site-level based on grazer behaviour and habitat condition. Traditionally, hill sheep overwintered in paddocks on the lower hills in Wales (Cunningham, 1979). Habitats with higher conservation importance and lower carrying capacities were most selected in winter, therefore, it is recommended that grazers are removed from areas of semi-natural hill vegetation during this period. On sites where fields of improved agricultural grassland are unavailable, creation of such areas could be considered to provide conservation support areas to the majority of the upland and peatland contained. Typically hill sites in western Ireland that do not already have fields of improved grassland are unlikely to have suitable sites for either improved grassland or livestock housing, in which case selling sheep at the start of winter and buying replacements in spring may be the only feasible option if conservation objectives are to be met.

Recommendations made above should not compromise the financial viability of hill farming, i.e. if extra costs are involved, farmers should be compensated accordingly. This enterprise is highly dependent on agri-environment payments which should continue to pay farmers to manage land for conservation but with revised management agreements, increasing the efficacy of agri-environment schemes in this sector based on new findings on grazer behaviour. Further studies are required on multiple study sites, with varying topography and vegetation assemblages, to obtain sufficient data on resource selection by hill sheep for inclusion as parameters in management models. Although this study investigated hill sheep selection on a mosaic of upland and peatland habitats, the same applications could be made to aid conservation decision-making on a wide variety of assemblages of habitats, plant communities and vegetation condition, and with a range of study animals.

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