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The impact of red deer on liverwort-rich oceanic heath vegetation

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Abstract

Background: There is concern about **increasing numbers of large herbivores including red deer (*Cervus elaphus*) but little is known** about their impact on bryophytes.

Aims: This study set out to determine the effect of different localised densities of red deer on the internationally important Northern Atlantic hepatic mat, **characteristic of oceanic heath vegetation, at four locations in the Scottish Highlands** where sheep have been absent for decades.

Methods: Thirty **7 m x 7 m** plots were randomly located in each study area. The standing crop dung pellet group count method was used to estimate red deer density. Species richness, diversity and cover of hepatic mat liverworts were obtained from **1 m x 1 m** quadrats placed at random within the sample plots. *Calluna vulgaris* cover, ericoid height, rock cover, gradient and altitude were also recorded.

Results: Model simplification in ANCOVA revealed a consistent pattern of decreasing cover of hepatic mat and *Calluna* with increasing red deer density at all four study areas. Northern Atlantic hepatic mat cover, diversity and species richness were positively correlated with *Calluna* cover.

Conclusions: The data suggest that *Calluna* cover is reduced (through trampling and browsing) at high local densities of red deer which has had cascading effects on the Northern Atlantic hepatic mat. Alternative explanations are discussed.

Key-words: Browsing, *Calluna vulgaris*, *Cervus elaphus*, conservation, Northern Atlantic mixed hepatic mat, species richness, trampling

Introduction

Oceanic heath is a rare habitat of international importance and high conservation value (Averis et al. 2004; Rothero 2010). **It is characterised by colourful mixtures of large leafy-liverwort species growing below the dwarf-shrub canopy (Rodwell 1991; Averis et al. 2004), collectively described as the mixed Northern Atlantic hepatic mat (Ratcliffe 1968). This liverwort community is comprised of combinations of any number of 16 species (Table 1) growing in close association (Averis 1992), all of which require an oceanic climate. Eleven of these liverworts have a Northern Atlantic distribution (Ratcliffe 1968) and only occur together in northwest Scotland (Averis 1992). Otherwise, the species which make up the Northern Atlantic component of the hepatic mat have disjunct world distributions (Schuster 1979; Hodgetts 1997; Long 2010; Rothero 2010). There are good stands of the mixed Northern Atlantic hepatic mat in western Ireland, the Faroe Islands and in southwest Norway but the most extensive and species-rich examples occur in the northwest Highlands of Scotland** (Crundwell 1970; Rothero 2010; Hodd and Sheehy Skeffington 2011). **This paper focuses on oceanic heath described by the H21b *Mastigophora woodsii-Herbertus hutchinsiae* sub-community of the *Calluna vulgaris–Vaccinium myrtillus–Sphagnum capillifolium* heath in the National Vegetation Classification (Rodwell 1991). However, the term oceanic heath could also be applied to the H20c *Bazzania tricrenata-Mylia taylorii* sub-community of the *Vaccinium myrtillus-Racomitrium lanuginosum* heath (Flagmeier et al. 2013) which occurs at higher altitudes.**

Burning and grazing are well known threats to the liverwort-rich oceanic heath (McVean and Ratcliffe 1962; Ratcliffe 1968; Birks 1973; Hobbs 1988; Averis 1994; Averis et al. 2000; Elkington et al. 2001; Rothero 2003; Averis et al. 2004; Porley and Hodgetts 2005; Long

2010; Hodd and Sheehy Skeffington 2011) though damage by these means has not been quantified (Averis 1992). The effects of overgrazing by sheep are well documented, particularly in Ireland (Blockeel 1995; Porley and Hodgetts 2005; Holyoak 2006; Long 2010), but the impact of grazing by red deer (*Cervus elaphus*) on the oceanic heath is less well known. **Greater impact on heather condition within heather-grass mosaics is thought to occur when deer graze in the absence of sheep compared to mixed grazing situations (DeGabriel et al. 2011).** With numbers of red deer in the Highlands almost doubling since the 1970s as a result of reduced sheep stocks and climate change (Clutton-Brock et al. 2004), we need to know if this large herbivore is a threat to the mixed Northern Atlantic hepatic mat.

The ecological amplitude of the Northern Atlantic hepatic mat is limited (Hobbs 1988; Hill et al. 1991; Paton 1999; Atherton et al. 2010; Hodd and Sheehy Skeffington 2011). It occurs in mountainous regions with an oceanic climate, subject to mild winters and cool summers, high atmospheric humidity and in receipt of $\geq$ 1 mm of rain on $\geq$ 220 days year^{-1} (McVean and Ratcliffe 1962; Ratcliffe 1968; Hobbs 1988). Relatively steep, rocky slopes and cliffs with an aspect between north-west and east, which remain shaded for most of the day, are particularly favourable to the hepatic mat (Ratcliffe 1968; Rodwell 1991; Averis et al. 2004). However, anecdotal evidence suggests that oceanic heath was previously more widespread on flat ground in addition to steep slopes and the present distribution is a result of management history (McVean and Ratcliffe 1962; Hobbs 1988; Porley and Hodgetts 2005).

Long-distance dispersal is also extremely limited in the Northern Atlantic liverwort component of oceanic heath (Hodd and Sheehy-Skeffington 2011). Sexual reproduction has only been reported once in the British Isles (Averis 1994) and few of the scarce hepatic mat species produce specialised vegetative propagules such as gemmae (Paton 1999). Fragmentation of the gametophyte is the only mechanism that might enable the establishment of new populations and this is thought to be slow and unpredictable (Rothero 2003). Therefore, this unique community of liverworts is very vulnerable to the damaging effects of overgrazing and muirburn (Hodd and Sheehy Skeffington 2011).

According to anecdotal evidence, the oceanic heath is able to withstand low levels of grazing but high numbers of large herbivores eventually converts the oceanic heath to grassland (Ratcliffe 1968; Averis et al. 2000; Averis et al. 2004). Without a canopy of heather there is a reduction in atmospheric humidity and many of the rare Northern Atlantic liverworts are unable to persist (Averis et al. 2000). Grazing by red deer is thought to have reduced the extent of oceanic heath on Ben More Assynt and Beinn Bhàn according to Hobbs (1988). However, limited evidence exists to suggest that red deer cause extensive changes to the distribution of upland plant communities other than through the inhibition of woodland regeneration (Clutton-Brock et al. 2002) but this may simply reflect the lack of studies that separate the effects of deer and sheep grazing. It is also difficult to quantify damage to the oceanic heath even when the effects of burning and grazing are obvious in the field (Hobbs 1988).

In this study the non-random distribution of red deer within an area of landscape is exploited to examine how this herbivore may be impacting on the oceanic heath community. The interaction between herbivores and vegetation is localised within a landscape but remains an important driver of change (Gordon et al. 2004). Therefore, it is expected that within an area of heather moorland there will be places that are more intensively used than others. The sensitivity of the landscape is influenced by the patchiness of vegetation because change is fastest at the boundaries between plant communities (Milne and Hartley 2001). For example, red deer prefer to browse *Calluna* at the edge of grass patches in upland heath leading to loss of heather cover (Hester and Baillie 1998; Gordon et al. 2004). Patches of Northern Atlantic hepatic mat were expected to be at lower risk from the effects of trampling or loss of the dwarf-shrub layer in places where it was awkward for deer to access **or less attractive for grazing**.

It was predicted that the mixed Northern Atlantic hepatic mat would be impoverished (as a result of reduced heather cover and direct trampling damage) where intensity of usage by red deer was locally high. This study therefore compared areas of oceanic heath in northwest Scotland under contrasting management regimes. Greater impact on the oceanic heath vegetation was expected in study areas on sporting estates where estimated mean deer density for the whole property was higher than on nature reserves. It is hoped that the models presented here will be useful in predicting the impacts of different densities of red deer **in other areas of the Highlands** where liverwort-rich oceanic heath occurs.

Method

Site Description

Eight areas of oceanic heath vegetation were identified from historical and personal records in the vicinity of Loch Maree, Wester Ross (Scotland). Two of these areas were selected at random from a sporting estate and two from neighbouring nature reserves (Table 2). At each location, the study area stretched for a distance of 1 km below north- to northwest- facing crags. Sheep have been absent from all of these areas for over 30 years but past grazing has been more intensive on the Letterewe Estate (Averis and Averis 1998, Milner et al. 2002). Doire Crionaich appears to have suffered most damage from historical management (personal observation). However, oceanic heath vegetation did still exist within this study area, in an area of large block scree, in heath close to the cliffs below a remnant hanging wood and in the lower slopes of Coire nan Laogh. Hence, random sampling was confined to these particular sites at this location rather than the hillside as a whole. Each study area was subject to the same oceanic climate (Meteorological Office 2013) and altitude of the sample plots was in the range 237–502 m. The mixed hepatic mat is not affected by the chemical composition of the underlying rock and can occur over a variety of substrates including quartzite, sandstone, base-rich mica-schists and basalt (Rodwell 1991; Averis 1994).

Procedure

Grid references were selected at random for the bottom left-hand corner for each of thirty sample plots located within each study area. For those sample plots landing on an unsuitable site such as an area of open scree, or in the middle of a flush system, either a new plot was selected in the vicinity at random from a number of possible plots or an entirely new grid reference was taken. Each plot constituted a 7 m x 7 m area marked out with tape measures.

This was searched thoroughly for red deer dung pellet groups according to the standing crop dung pellet group count method (De Nahlik 1992; Mayle et al. 1999) **as a proxy for estimating red deer density. Considerable effort was given towards searching for pellet groups – systematically walking 1 metre strips at a time within the 7 m x 7 m sample plot, parting vegetation with the hands and looking between boulders as necessary – to reduce the chances of missing any**. By taking enough randomly placed sample plots within each study area, it was hoped to get a range of red deer usage values with which to correlate against impact to the hepatic mat. Fieldwork was carried out in spring (2012) **before new vegetative growth made finding dung pellet groups more difficult**.

Percentage rock cover for each sample plot was estimated by eye and altitude was recorded using a GARMIN eTrex Legend GPS device. The sample plot was divided up into squares of area 1 m^2 and each allocated a number between 1 and 49 from which one was selected at random. If this quadrat landed entirely on a large rock or scree then a new square was selected at random. The percentage-cover of each bryophyte and lichen species (and dominant higher plant) within this 1 m x 1 m quadrat were estimated visually using a grid with 0.1 m x 0.1 m squares. Total hepatic mat cover was recorded *in situ* but the cumulative total of Northern Atlantic liverworts within the mat was calculated later. Mean ericoid height was obtained based on ten measurements with a metre rule at regular intervals in a pre-determined diagonal. **The nearest stem to the rule was measured.** Hepatic mat species height was measured in a similar way. Micro-gradient and percentage rock cover were also recorded from each of these quadrats. For quickness, the micro-gradient was scored on a scale of 1 – 5 that increased with steepness from the horizontal to the vertical. A 1 m x 1 m quadrat was used for this fieldwork owing to the awkward nature of the terrain where any size larger would have made recording difficult.

Bell et al. (2012) was observed for the naming of *Herbertus borealis* and *H. hutchinsiae* but the nomenclature of all other bryophytes followed Hill et al. (2008). Nomenclature followed Macdonald and Barrett (1993) for mammals and Stace (2010) for vascular plants.

Analysis

The dung pellet group count data for each 49 m^2 sample plot were converted into equivalent red deer densities (km^{-2}) using the dung pellet group count–deer density graph as presented in De Nahlik (1992). By monitoring the life expectancy of a number of fresh dung pellet groups in oceanic heath habitat at Letterewe, a decay rate of between 6 and 12 months was assumed. The defaecation rate was taken to be 25 dung pellet groups per day (which gives a more conservative estimate of red deer density). Whilst this method of estimating red deer was **internally consistent it is only** precise to ± 20% (Mayle et al. 1999) so the estimates of deer density in this research should be treated with some caution.

Dominance (species identity), species richness and Shannon diversity (evenness) for all cryptogams within each quadrat and for only the Northern Atlantic members of the hepatic mat community were calculated prior to analysis. **Dominance was calculated by dividing the cover of the most abundant cryptogam species with total cover of all cryptogams within a quadrat.** Percentage cover data were arcsine transformed prior to analysis using R version 2.11.1 (R Development Core Team 2010). ANOVA was used to establish whether there were differences in the means of the explanatory variables such as *Calluna* cover, red deer density and ericoid height between locations. *A priori* orthogonal contrasts were used to compare the two study areas in the Letterewe Forest with those sites managed specifically for the natural heritage (Beinn Eighe and Liathach), and to look for differences in means between the individual locations.

Model simplification in ANCOVA identified which of the main effects had the most explanatory power for each of the relevant response variables. For continuous response variables, such as arcsine cover of hepatic mat, this was done using a Linear Model (LM) with normal errors. For count data such as Northern Atlantic liverwort species richness, model simplification was performed in a Generalised Linear Model (GLM) with a quasipoisson error structure because of over-dispersion in the response. The explanatory variables considered for use in the maximal models included those that were categorical, namely location and gradient and those that were continuous such as altitude, *Calluna* cover, red deer density, rock cover and mean ericoid height as appropriate. Inspection of boxplots, scatter graphs and tree models assisted with the initial parameterisation of the **maximal** models. To avoid the problems associated with over-parameterisation, the **maximal** model was constructed following the guidance in Crawley (2005). This pragmatic approach required inclusion of the quadratic functions for those continuous explanatory terms that actually showed evidence of curvature and only the significant two-way interactions (from separate models with randomly selected sets of the interaction terms with all of the main effects). Three-way interactions were also included at the outset if the variables were already involved in important two-way interactions. Models were compared consecutively using ANOVA in order to justify the removal or retention of explanatory terms in a stepwise manner. Each minimum adequate model (MAM) that resulted from this process was tested for goodness of fit. The predict function in R was used to plot the model from the data.

Results

A total of 104 cryptogam species were recorded from the 120 quadrats (see Appendix S1). *Sphagnum capillifolium* ssp. *rubellum* and bulky pleurocarpous mosses such as *Hylocomium splendens*, *Hypnum jutlandicum*, *Racomitrium lanuginosum* and the liverwort *Diplophyllum albicans* were present in the majority of quadrats. *Calluna vulgaris* was absent from just one quadrat. Doire Crionaich had the greatest cryptogam species richness overall (Table 3). However, there were fewer species comprising the hepatic mat at this location due to the lower number of nationally scarce Northern Atlantic liverworts (although *Scapania nimbosa* and *Bazzania pearsonii* were seen outside of quadrats). *Anastrophyllum donnianum* was recorded from a handful of quadrats at Beinn Eighe and once at Bealach a Chùirn. The hepatic mat at Beinn Eighe included the endemic and nationally rare *Herbertus borealis*.

Explanatory variables were compared across locations using ANOVA (Figure 1). There was no significant difference in the *a priori* orthogonal contrast that compared mean red deer density between the two locations from a sporting estate with those managed for conservation. However, red deer density was significantly lower at Beinn Eighe compared to Liathach ($P = 0.019$) and significantly lower at Bealach a Chùirn compared to Doire Crionaich ($P = 0.004$). There was no significant difference in mean arcsine *Calluna* cover between locations. The *a posteriori* orthogonal contrasts show mean ericoid height to be significantly taller ($P < 0.001$) at Beinn Eighe than any of the other locations. Graminoid cover was significantly lower at Beinn Eighe compared to the other three locations combined ($P < 0.001$) after *a posteriori* orthogonal contrasts were applied.

The intercept in the MAM for *Calluna* cover was 1.048 and the estimate for the explanatory term of red deer density was –0.008 ± 0.001 (standard error) indicating the highly significant negative relationship ($P < 0.001$) between these variables (Figure 2). Rock cover also remained in the MAM with an estimate of –0.451 ± 0.113 and indicated a significant negative relationship ($P < 0.001$) with *Calluna* cover within quadrats. There was a significantly greater cover of *Calluna* in quadrats from the steepest gradient (estimate 0.379 ± 0.181) compared to those approaching the horizontal in the same model ($P = 0.039$). This model accounted for 41.3% of the variation in the data and had a reasonable goodness of fit with linearity in the normal errors and no obvious heteroscedasticity in the residuals. The MAM for ericoid height (with intercept 0.409) was similar in that the negative relationship with red deer density was highly significant ($P < 0.001$) with an estimate of –0.002 ± 0.0004. There was a significant negative relationship with rock cover in this model and a significant interaction between location and altitude (P = 0.005) – in which ericoid height was much lower at altitudes above 450 m in the study area at Beinn Eighe. Ericoid height at Beinn Eighe (estimate 1.49 ± 0.50) was also shown to be significantly taller compared to Bealach a Chùirn (P = 0.003).

There were no clear trends or differences in total cryptogam species diversity, dominance or Northern Atlantic liverwort dominance. Mean height of hepatic mat species within quadrats was significantly greater at Beinn Eighe and Liathach compared to Bealach a Chùirn and Doire Crionaich ($P < 0.05$) according to *a priori* orthogonal contrasts. As this response variable was auto-correlated with hepatic mat cover no further analysis was attempted for hepatic mat height.

The intercept was 0.289 in the MAM for hepatic cover (Figure 3). There was a highly significant negative relationship ($P < 0.001$) between hepatic mat cover and red deer density (estimate –0.011 ± 0.003). The positive correlation between hepatic mat cover and *Calluna* cover (estimate 0.839 ± 0.258) was also significant ($P = 0.002$) in this MAM. There were significant quadratic functions (*P* < 0.05) for each of these explanatory variables remaining in the MAM. The model accounts for 49.2% of the variation in the data but there is slight curvature in the Normal error plot and a hint of heteroscedasticity in the variance-mean relationship. A similar outcome was achieved in the MAM for total cover of only the Northern Atlantic members of the hepatic mat, for which the intercept was 0.491. The estimate for the explanatory variable of red deer density was –0.013 ± 0.003 suggesting a significant negative relationship with Northern Atlantic liverwort cover (*P* < 0.001). There was also a significant positive relationship (*P* = 0.009) with *Calluna* cover (estimate 0.207 ± 0.078. Location was an important main effect in this model. The *a priori* contrasts for location showed a significantly greater (*P* = 0.006) arcsine cover of Northern Atlantic liverworts at the Beinn Eighe and Liathach study areas compared to those at Letterewe (estimate 0.059 ± 0.021). One significant positive quadratic function remained in the model for red deer density (*P* = 0.047). This model accounted for 46.9% of the variation in the data but again goodness of fit was disappointing with some heteroscedasticity in the residual errors plot and slight curvature in the normal errors

A highly significant positive relationship with *Calluna* cover (*P* < 0.001) is suggested by the MAM for Northern Atlantic liverwort diversity (estimate 0.543 ± 0.125) for which the intercept is –0.493 (Figure 4). Altitude is also an important explanatory term (*P* = 0.003) for Northern Atlantic liverwort diversity (estimate 0.002 ± 0.001). This simple model accounts for just 21.0% of the variation in the data and **goodness of fit was inadequate.**

Figure 5 illustrates the MAM for Northern Atlantic liverwort species richness for which the intercept was 0.795. Location was a significant main effect and *a priori* orthogonal contrasts demonstrate a significantly higher (*P* = 0.005) number of Northern Atlantic liverwort species in quadrats from Beinn Eighe and Liathach compared to those from Letterewe (estimate

0.145 ± 0.051). **This may have more to do with historical management (more intensive sheep farming at Letterewe) than present estimates of mean deer density (those at Liathach were more similar to the Letterewe property compared to Beinn Eighe).** There was no significant difference in Northern Atlantic species richness between Beinn Eighe and Liathach ($P = 0.092$) nor between Bealach a Chùirn and Doire Crionaich ($P = 0.387$). The MAM indicated that *Calluna* cover (estimate 0.689 ± 0.001) was a significant explanatory term ($P < 0.001$) and there was a highly significant negative relationship ($P = 0.005$) with red deer density (estimate –0.009 ± 0.003). The explanatory term altitude had been removed during the simplification process. This model accounted for 32.4% of the variation in the data and there was an acceptable goodness of fit.

Model simplification was carried out for the cover of the most frequent individual members of the Northern Atlantic component of the hepatic mat. Red deer density, *Calluna* cover and location were consistently important explanatory terms as shown in the MAM for *Herbertus hutchinsiae* (Figure 6) for which the intercept was –0.001. There was a highly significant ($P < 0.001$) negative relationship with red deer density (estimate –0.005 ± 0.001) and a significant positive correlation ($P = 0.009$) with *Calluna* cover (estimate 0.726 ± 0.271) for which there was also a significant quadratic function ($P = 0.030$). Location was a significant main effect and *a posteriori* orthogonal contrasts demonstrate a significantly greater ($P < 0.001$) abundance of *H. hutchinsiae* in quadrats from the study areas at Beinn Eighe, Doire Crionaich and Liathach compared to those from Bealach a Chùirn. There was no significant difference in the remaining two orthogonal contrasts. The MAM accounted for 38.8% of the variation in the data. The normal errors were reasonably linear but there was serious heteroscedasticity in the variance-mean relationship.

Repeating the model simplifications with suitably transformed variables when necessary did not result in any improvement in the goodness of fit. However, the high significance of the main effects in the MAMs and the straightforward interpretations **remove any cause for concern**. **Full ANCOVA tables for each MAM described above are given in Appendix S2.**

Discussion

Calluna cover was an important explanatory variable in most of the models – being positively correlated with species richness, Shannon diversity and total cover of the Northern Atlantic component of the hepatic mat, total hepatic mat cover and abundance of individual species within the mat. The dwarf-shrub canopy amplifies the effect of a constant atmospheric humidity that is fundamental to the ecology of the Northern Atlantic hepatic mat (Hobbs 1988). There was no significant difference in mean *Calluna* cover between study areas but the model suggests that *Calluna* cover is locally reduced within each study area – especially where red deer density was concentrated. This was particularly noticeable in those sample plots of oceanic heath that were in transition to grassland associated with the edges of existing patches of grassland. This edge effect is consistent with the literature since red deer are known to exert a greater impact on heather where it borders patches of grassland than elsewhere in a heathland (Clarke et al. 1995ab; Hester and Baillie 1998; Milne and Hartley 2001; Gordon et al. 2004). Grassland is a poor habitat for the Northern Atlantic hepatic mat community (Ratcliffe 1968) with reduced humidity and no protection from extremes of temperature and insolation. However, there was a wide range of estimated red deer densities at each of the four study areas based on the counts of dung pellet groups in the sample plots. This suggests that the Northern Atlantic mixed hepatic mat has continued to persist in parts of the oceanic heath **that are** less frequently used by red deer at all four study areas.

It is acknowledged that the correlation between high deer dung counts and low heather cover could merely reflect deer preferences. Nonetheless, there was a consistent pattern of decreasing cover of Northern Atlantic hepatic mat with increasing numbers of red deer at all four study areas. Higher dung counts at the most impacted sample plots clearly indicated those places in the study areas that were favoured by red deer. The model predicts a 50%

lower hepatic mat cover within quadrats in sample plots where estimated local red deer density was equivalent to 25 km^{-2} compared to those quadrats occurring in sample plots where no dung was present. *Calluna* cover was half as abundant in quadrats where estimated local red deer density was equivalent to 55 km^{-2} within sample plots compared to those where no dung was found. This is consistent with Grant et al. (1981) who showed that browsing **of upland heath** by high densities of red deer in enclosures significantly reduced heather cover **as a result of heavy utilisation. This suggests that locally high densities of red deer are capable of degrading oceanic heath by removing the heather canopy. DeGabriel et al. (2011) demonstrated a positive correlation between red deer dung density and heather utilistaion at 16 upland sites across Scotland. It was also shown that in the absence of competition from sheep, heather was shorter and there were a significantly higher number of red deer dung pellet groups within the experimental pots (DeGabriel et al. 2011). DeGrabriel et al. (2011) warned that heather condition could be compromised as a result of increasing numbers of red deer – particularly at the edges of grass patches where deer had initially been attracted by the presence of favoured grasses. This lends further support to the notion that high numbers of red deer are** reducing dwarf-shrub cover and height locally in oceanic heath with cascading effects on the Northern Atlantic hepatic mat. It should be emphasised that these high deer density estimates were for small localised areas within the study area and not for the whole property (where estimates of red deer numbers were much lower) and there is a large margin for error.

An alternative argument is that red deer are seeking habitats where the Northern Atlantic hepatic mat is already absent or actively selecting against places where it is present. This theory does not explain those sample plots in which the hepatic mat was abundant below a canopy of *Calluna* except where a deer path crosses the plot and regular trampling has destroyed the mat. At other locations, the hepatic mat was present below one or two remnant patches of mature *Calluna* when the rest of what would have been suitable habitat had clearly been browsed to grassland. Quadrats landing on these surviving patches of hepatic mat within an otherwise severely grazed sample plot may account for the curvature in this model (Figure 3). A negative linear relationship between hepatic mat cover and red deer density (such as that seen in Figure 6) would more closely reflect reality based on anecdotal observations in the literature (Ratcliffe 1968; Blockeel 1995; Averis et al. 2000; Holyoak 2006; Long 2010). If these grass patches (with *Calluna* grazed low) were fenced off then evidence from elsewhere suggests that dwarf-shrub communities would come to dominate what was previously grassland (Milne et al. 1998) and create conditions for possible recolonisation of the hepatic mat from nearby. Manipulative experiments using enclosures of known deer density would still be needed to confirm what the correlative data are suggesting. However, these would be expensive to **establish and maintain**, cause severe damage to an important plant community and would have to be replicated. Enclosures on the north-facing slopes of rocky, mountainous terrain would also be subject to damage by rock fall, confounded by changes in the snow regime and create access issues.

The models suggest an intermediate *Calluna* cover is optimal for hepatic mat and *H. hutchinsiae* abundance. This accounts for those situations where the ***Calluna*** canopy became dense enough to exclude the ground layer. Growth of hepatic mat is known to favour the space between the dwarf-shrubs rather than immediately below them (Ratcliffe 1968). In some heavily grazed situations at the base of dripping crags, the extra shelter and humidity permits the survival of hepatic mat species without the need for a protective canopy of ericoid shrubs. This may explain why a few quadrats had higher than expected hepatic mat cover in the near-absence of *Calluna*. There were also several quadrats with lower than expected hepatic mat cover at very low deer densities. Random quadrat placement and the discontinuous nature of the hepatic mat meant that other species associated with oceanic heath were often dominant within a quadrat. Power analysis ensured a sufficient number of samples were taken at each study area in order to overcome this problem and discover genuine trends in the data. Caution is advised when using these models since they only explain < 50% of the variation in the data and there should be no extrapolation beyond their limits.

The negative relationship between species richness of the Northern Atlantic component of the hepatic mat and red deer density **implies that the total area covered by this liverwort community is not reduced.** Instead, increasing usage by red deer **is correlated with an** impoverishment of species that comprise the hepatic mat. This is a likely response to a changed microhabitat following the removal of the *Calluna* cover by the activities of the herbivore. Since the influence of altitude had been removed during model simplification the lower number of species in quadrats from the study areas at Letterewe might have something to do with previous management regimes. This supports Averis (1992) who suggested that it would be worthwhile trying to correlate numbers of hepatic mat species against intensity of management using estate records across Scotland. However, this would not necessarily describe the condition or extent of the hepatic mat cover at each site and may be misleading.

Main effects such as rock cover, gradient, and ericoid height were all removed during model-simplification. Hobbs (1988) associated hepatic mat with a tall canopy of *Calluna* but there were several sample plots in the present study where the hepatic mat thrived beneath a rather low canopy of *Calluna* at higher altitudes and situations where a tall (but opened) ericoid layer had an impoverished ground flora due to recent trampling by red deer. Alternatively, ericoid height may have been confounded with the differences associated with location since it was taller at Beinn Eighe and Liathach compared to the Letterewe study areas. The presence of rocky terrain and boulder fields are probably more important at the landscape scale rather than in individual quadrats. Rocky situations and stabilised scree are known to confer enhanced humidity, shade and protection from fires and trampling by grazing animals (Ratcliffe 1968; Hobbs 1988). It was anticipated that steeper gradients might be less susceptible to trampling but hepatic mat was occasionally found in quadrats placed on flat ground amid block scree and so this explanatory variable was nullified.

The significant positive relationship between altitude and Shannon diversity of the Northern Atlantic component of the hepatic mat is explained by the increasing presence of species that have more exacting requirements (Averis 1994). Species such as *Anastrophyllum donnianum*, *Scapania nimbosa* and S. *ornithopodioides* are better able to compete with other hepatic mat liverworts as temperatures become cooler with increasing altitude (Averis 1994). These species are more common in the hepatic mat associated with the H20c *Bazzania tricrenata-Mylia taylorii* sub-community of the *Vaccinium myrtillus-Racomitrium lanuginosum* heath (Rodwell 1991) that occurs at higher altitudes. The dataset only goes up to approximately 500 m so it would be unwise to extrapolate beyond this point. The low amount of variation accounted for by this model suggests that there are other factors influencing diversity which were not measured in the field.

Estimates of red deer using the study areas were much greater than the averages given for each property as a whole. This was expected since north-facing slopes offer shelter to red deer from the stronger south-westerly winds (Fraser Darling 1937). Consequently, red deer can become concentrated at specific locations for periods of time. Milner et al. (2002) showed that red deer were not randomly distributed over any particular area at Letterewe because there was no relationship between habitat use and availability. This should be taken into account when decisions are being made on quotas for the deer cull rather than aiming for an average deer density for the whole property. The higher than expected mean red deer density in the study area at Liathach (where average deer density for the whole property is half that of Letterewe) might be explained in terms of the local Torridonian sandstone topography channelling deer passage through specific routes around and below cliffs. Here the difference in geology is confounding comparison of deer impact between different estates but it did serve to demonstrate what can happen to the habitat where deer numbers are locally higher at any one study area.

There is a frequent turn-over of individuals in the dynamic hepatic mat community as it responds to changes in its habitat following rock-falls and hill-creep or tracking the growth phase of *Calluna* (Averis 1994). At sites where average deer densities for a property are low and oceanic heath vegetation is extensive like that at Beinn Eighe, the localised impacts of red deer activity contribute to the unstable nature of the mountain habitat in which the hepatic mat occurs. However, the data presented here suggest that high densities of red deer are a potential threat to the Northern Atlantic hepatic mat. Trampling by the regular passage of deer and a reduction in *Calluna* cover is inimical to this rare liverwort community. This conflicts with Moore et al. (In press) who demonstrated that an absence of red deer within an exclosure at Knoydart led to a reduction in liverworts associated with the hepatic mat. However, this was at sea level and birch regeneration was dense and rapid. Where the hepatic mat occurs on steep, north-facing, rocky slopes in the mountains, there is unlikely to be a threat from dense tree regeneration due to lack of a seed source and difficult growing conditions. Oceanic heath is thought to be self-perpetuating in these situations since *Calluna* is able to grow from adventitious roots without the need for grazing or burning management (Averis 1994). Our data support Rothero (2006) who suggested that a reduction in grazing of these dwarf-shrub communities would benefit liverworts associated with the Northern Atlantic hepatic mat. At sites where the hepatic mat has already been eradicated, no amount of deer culling or subsequent regrowth of heather is going to bring it back naturally, due to the limited means of dispersal and establishment among its constituent species.

Locally high numbers of red deer within areas of oceanic heath at four locations in the northwest Highlands are correlated with impoverishment of the Northern Atlantic hepatic mat. Direct trampling damage and browsing of *Calluna* by red deer are thought to be the cause of this relationship. Land-managers with an interest in conserving this internationally important liverwort community should consider the non-random distribution of red deer when deciding on a suitable average deer density for their property. **This is consistent with Rothero (2010) who recommended that large herbivores should be managed to prevent loss of heather cover where the mixed Northern Atlantic hepatic mat occurs – informed by regular monitoring. Other ways of reducing grazing pressure are encouraged rather than exclosures but if these are used then regular monitoring of the ground flora would be necessary to avoid loss of the charismatic liverworts (Rothero 2010). Avoidance of muirburn is essential near stands of the mixed Northern Atlantic hepatic mat – which should all be listed on relevant documents to assist with site management (Rothero 2010).**

Supplemental data

Appendix S1 may be accessed online

Appendix S2 may also be accessed online

References

Atherton I, Bosanquet S, Lawley M. 2010. Mosses and liverworts of Britain and Ireland: A field guide. British Bryological Society.

Averis A. 1992. Where are all the hepatic mat liverworts in Scotland? Botanical Journal of Scotland 46:191–198.

Averis A. 1994. The ecology of an Atlantic liverwort community. [PhD Thesis]. [Edinburgh (Scotland)]: University of Edinburgh.

Averis ABG, Averis AM. 1998. Vegetation survey of Beinn Eighe, Wester Ross, 1997. Unpublished Report for Scottish Natural Heritage.

Averis ABG, Averis AM, Birks HJB, Horsfield D, Thompson DBA, Yeo MJM. 2004. An illustrated guide to British upland vegetation. Peterborough (UK): Joint Nature Conservation Committee.

Averis ABG, Averis AM, Horsfield D, Thompson DBA. 2000. The upland vegetation of the Western Isles, Scotland. Scottish Natural Heritage Research Survey and Monitoring Report No. 164.

Bell D, Long DG, Forrest AD, Hollingsworth ML, Blom HH, Hollingsworth PM. 2012. DNA barcoding of European *Herbertus* (Marchantiopsida, Herbertaceae) and the discovery and description of a new species. Molecular Ecology Resources 12:36–47.

Birks HJB. 1973. Past and present vegetation of Skye. Cambridge (UK): Cambridge University Press.

Blockeel TL. 1995. Summer field meeting, 1994, second week, Clifden. Bulletin of the British Bryological Society 65:12–18.

British Geological Survey. 1962. Torridon – Sheet 82. Southampton (UK): Ordnance Survey.

British Geological Survey. 1962. Inverbroom – Sheet 92. Southampton (UK): Ordnance Survey.

Clarke JL, Welch D, Gordon IJ. 1995a. The influence of vegetation pattern on the grazing of heather moorland by sheep and deer. I. The location of animals on grass/heather mosaics. Journal of Applied Ecology 32:166–176.

Clarke JL, Welch D, Gordon IJ. 1995b. The influence of vegetation pattern on the grazing of heather moorland by sheep and deer. II. The impact on heather. Journal of Applied Ecology 32:177–186.

Clutton-Brock TH, Crawley MJ, Milner JM. 2002. Deer in the Highlands. In: Milner JM, Alexander J, Griffin C, editors. A Highland deer herd and its habitat. London (UK): Red Lion House. p. 237–255.

Clutton-Brock TH, Coulson T, Milner JM. 2004. Red deer stocks in the Highlands of Scotland. Nature 429:261–262.

Crawley MJ. 2005. Statistics: An Introduction using R. Chichester (UK): John Wiley & Sons Ltd.

Crundwell AC 1970. *Herbertus borealis*, a new species from Scotland and Norway. Transactions of the British Bryological Society 6:41–49.

Daniels MJ. 2006. Estimating red deer *Cervus elaphus* populations: an analysis of variation and cost effectiveness of counting methods. Mammal Review 36:235–247.

DeGabriel JL, Albon SD, Fielding DA, Riach DJ, Westaway S, Irvine RJ. 2011. The presence of sheep leads to increases in plant diversity and reductions in the impact of red deer on heather. Journal of Applied Ecology 48:1269-1277.

De Nahlik AJ. 1992. Management of deer and their habitat – principles and methods. Gillingham, Dorset (UK): Wilson Hunt.

Elkington T, Dayton N, Jackson DL, Strachan IM. 2001. National vegetation classification: field guide to mires and heaths. Peterborough (UK): Joint Nature Conservancy Council.

Flagmeier M, Long DG, Genney D, Hollingsworth PM, Woodin SJ. 2013. Regeneration capacity of oceanic-montane liverworts: implications for community distribution and conservation. Journal of Bryology. 35:12–19.

Fraser Darling F. 1937. A herd of red deer. London (UK): Oxford University Press.

Gordon I J, Hester AJ, Festa-Bianchet M. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.

Grant SA, Hamilton WJ, Souter C. 1981. The responses of heather dominated vegetation in North-East Scotland to grazing by red deer. Journal of Ecology 69:189–204.

Hester AJ, Baillie GJ. 1998. Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. Journal of Applied Ecology 35:772–784.

Hill MO, Blackstock TH, Long D, Rothero G. 2008. A checklist and census catalogue of British and Irish bryophytes. Cheshire (UK): British Bryological Society.

Hill MO, Preston CD, Smith AJE. 1991. Atlas of the bryophytes of Britain and Ireland Vol. 1 Liverworts. Colchester (UK): Harley Books.

Hobbs AM. 1988. Conservation of leafy liverwort-rich *Calluna vulgaris* heath in Scotland. In: Usher MB, Thompson DBA, editors. Ecological change in the uplands. Oxford (UK): Blackwell Scientific Publications. p. 339–343.

Hodd R, Sheehy Skeffington MJ. 2011. Mixed northern hepatic mat: a threatened and unique bryophyte community. Field Bryology 104:2–11.

Hodgetts NG. 1997. Atlantic bryophytes in Scotland. Botanical Journal of Scotland 49:375–385.

Holyoak DT. 2006. Progress towards a species inventory for conservation of bryophytes in Ireland. Proceedings of the Royal Irish Academy 106B:225–236.

Laughton Johnston J, Balharry D. 2001. Beinn Eighe: The mountain above the wood. Edinburgh (UK). Birlinn Ltd.

Long D. 2010. The tragedy of the Twelve Bens of Connemara: is there a future for *Adelanthus lindenbergianus*? Field Bryology 100:2–8.

Long DG, Paton JA, Squirrell J, Woodhead M, Hollingsworth PM. 2006. Morphological, ecological and genetic evidence for distinguishing *Anastrophyllum joergensenii* Schiffn. and *A. alpinum* Steph. (Jungermanniopsida: Lophoziaceae.). Journal of Bryology 28:108–117.

Macdonald D, Barrett P. 1993. Mammals of Britain & Europe. London (UK): HarperCollinsPublishers.

Mayle BA, Pearce AJ, Gill RMA. 1999. How many deer? A field guide to estimating deer population size. Forestry Commission Field Book 18. Edinburgh (UK): Forestry Commission.

McVean DN, Ratcliffe DA. 1962. Plant communities of the Scottish Highlands. Monograph No. 1 of the Nature Conservancy. London (UK): HMSO.

Meteorological Office. 2013. UK mapped climate averages. http://www.metoffice.gov.uk/climate/uk/averages/ukmapavge.html. Site accessed 07/08/2013.

Milne JA, Birch CPD, Hester AJ, Armstrong HM, Robertson A. 1998. The impact of vertebrate herbivores on the natural heritage of the Scottish uplands – a review. Scottish Natural Heritage Review No. 95.

Milne JA, Hartley SE. 2001. Upland plant communities – sensitivity to change. Catena 42:333–343.

Milner J, Alexander J, Griffin C. 2002. A Highland deer herd and its habitat. London (UK) Red Lion House.

Moore O, Standen L, Crawley MJ. In press. The impact of red deer management on liverworts associated with the mixed hepatic mat community and other terrestrial cryptogams. Plant Ecology and Diversity. DOI: 10.1080/17550874.2013.815664.

Paton JA. 1999. The liverwort flora of the British Isles. Colchester (England): Harley Books.

Porley R, Hodgetts N. 2005. Mosses and liverworts. London (UK): HarperCollins Publishers.

Preston CD. 2006. A revised list of nationally scarce bryophytes. Field Bryology 90:22–30.

Preston CD. 2010. A revised list of nationally rare bryophytes. Field Bryology 100:32–40.

R Development Core Team 2010. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Ratcliffe DA. 1968. An ecological account of Atlantic bryophytes in the British Isles. New Phytologist 67:365–439.

Rodwell JS. 1991. British plant communities Volume 2: Mires and heaths. Cambridge (UK): Cambridge University Press.

Rothero G. 2003. Bryophyte conservation in Scotland. Botanical Journal of Scotland 55:17–26.

Rothero G. 2006. Bryophytes. In: Shaw P, Thompson DBA, editors. The nature of the Cairngorms: Diversity in a changing environment. Edinburgh (UK): The Stationery Office. p. 195–213.

Rothero G. 2010. Looking after Scotland’s oceanic heath. Back from the Brink Management Series. Plantlife Scotland.

Schuster RM. 1979. On the persistence and dispersal of transantarctic hepaticae. Canadian Journal of Botany 57:2179–2225.

Stace CA. 2010. New flora of the British Isles. 3rd ed. Cambridge (UK): Cambridge University Press.

Table 1. Liverworts associated with the mixed Northern Atlantic hepatic mat compiled using information from Ratcliffe (1968), Averis (1992) and Long et al. (2006). Nationally rare (NR) or nationally scarce (NS) status is given according to Preston (2006; 2010) and the other species are deemed to be more widespread in western Britain (present in > 100 10 km squares). This table was first published in Plant Ecology & Diversity by Moore et al. (In press) and is reproduced here with permission from Taylor & Francis.

Species	Conservation interest	Distribution
Adelanthus lindenbergianus	NR	Northern Atlantic
Anastrepta orcadensis		sub-Atlantic
Anastrophyllum alpinum	NR	Northern Atlantic
Anastrophyllum donnianum	NS	Northern Atlantic
Bazzania pearsonii	NS	Northern Atlantic
Bazzania tricrenata		Western British
Herbertus hutchinsiae		Northern Atlantic
Lepidozia pearsonii	NS	Northern Atlantic
Mastigophora woodsii	NS	Northern Atlantic
Mylia taylorii		Western British
Plagiochila carringtonii	NS	Northern Atlantic
Plagiochila spinulosa		sub-Atlantic
Pleurozia purpurea		Northern Atlantic
Scapania gracilis		sub-Atlantic
Scapania nimbosa	NS	Northern Atlantic
Scapania ornithopodioides	NS	Northern Atlantic

Table 2. Site details for each randomly selected study area of oceanic heath in Wester Ross, Scotland. Estimates of red deer numbers (at time of data collection) were provided by the relevant factor/reserve managers. Geological information came from maps produced by the British Geological Survey (1962).

Study area	Grid reference	Ownership	Management objective	Estimated mean red deer density on property (km^{-2})	Geology
Bealach a Chùirn	NG9674/9774	Letterewe Estate	Sporting (deer stalking/fishing)	9	Horneblende schist
Doire Crionaich	NG9376	Letterewe Estate	Sporting (deer stalking/fishing)	9	Horneblende schist
Liathach (Torridon)	NG9458	National Trust for Scotland	Conservation	4.7	Torridonian sandstone
Ruadh-stac Beag (Beinn Eighe)	NG9762	Scottish Natural Heritage	Conservation (National Nature Reserve)	≤ 3*	Quartzite

* Deer numbers have been reduced to a level that is permitting natural regeneration of native pine woodland (Eoghain Maclean pers. comm.) so this was taken to be ≤ 3 km^{-2} (which is the same as the deer numbers quoted for Beinn Eighe at the beginning of the 21st century) according to Laughton Johnston and Balharry (2001).

Table 3. Summary of cryptogam species richness (SR) in 30 quadrats at each of the four oceanic heath study areas in Wester Ross. Nationally rare or nationally scarce status is given according to Preston (2006; 2010)

	Number of species at each location			
Location	Bealach a Chùirn	Beinn Eighe	Doire Crionaich	Liathach
Total cryptogam SR	63	59	72	61
Hepatic mat SR	14	15	11	13
Northern Atlantic liverwort SR	9	10	6	8
Nationally scarce liverworts	**7**	**7**	**4**	**7**
Nationally rare liverworts	**0**	**1**	**0**	**0**

Figure 1. Bar charts showing (a) estimated mean red deer density for each study area based on the standing crop dung pellet group count procedure, (b) mean arcsine *Calluna vulgaris* cover, (c) mean ericoid height and (d) mean graminoid cover within 1 m^2 quadrats at each study area.

Figure 2. The relationship between *Calluna vulgaris* cover and estimated red deer density. The anomalous high cover of *Calluna* at the highest estimate of red deer density was from a quadrat on a vertical slope which avoided red deer impact. **Data have been back-transformed to give percentage cover values where appropriate.**

Figure 3. The MAM for hepatic mat cover fitted to the relevant data for the relationship with estimated red deer density (top) and *Calluna vulgaris* cover (below). **Data have been back-transformed to give percentage cover values where appropriate.**

Figure 4. The MAM for Northern Atlantic liverwort diversity is fitted to the relevant data for the relationship with *Calluna vulgaris* cover (top) and altitude (below). **Data have been back-transformed to give percentage cover values where appropriate.**

Figure 5. The MAM for Northern Atlantic liverwort species richness is fitted to the relevant data for the relationship with estimated red deer density (top) and *Calluna vulgaris* cover (below). The upper curve in each graph represents data from quadrats in the Beinn Eighe and Liathach study areas and the lower curve is for those data from Letterewe. **Data have been back-transformed to give percentage cover values where appropriate.**

Figure 6. The MAM for *Herbertus hutchinsiae* cover is fitted to the relevant data to show the relationship with estimated red deer density (top) and *Calluna* cover (below). The lower curve in each graph represents data from quadrats in the Bealach a Chùirn study area and the upper curve is for those data from the other three locations. **Data have been back-transformed to give percentage cover values where appropriate.**