Red deer (*Cervus elaphus*) grazing on vegetation mosaics

grazing patterns and implications for conservation management

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Declaration

I certify:

(a) that the thesis has been composed by me, and

(b) either that the work is my own, or, where I have been a member of a research group, that I have made a substantial contribution to the work, such contribution being clearly indicated, and

(c) that the work has not been submitted for any other degree or professional qualification except as specified.

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Lay Summary

Grazing is widely used as a tool in conservation management. However, the level of grazing which will keep plant community in ‘good’ condition to meet conservation goals is not well known for many types of plant community. Different plant communities may need different levels of grazing, and this increases the challenges facing conservation managers when more than one plant community is present at the same site. When more than one plant community is present, herbivores will tend to graze more on some than others. The preferred community is usually the one that offers the best trade-off between plant material with a high nutrient content and an abundant quantity of digestible plant material. Where herbivores choose to graze is also influenced by other factors, for example they may graze more in areas that are sheltered, or close to water. Grazing on a plant community that is less preferred by herbivores is often increased within a few metres of the most preferred community.

The effect of plant community layout on the pattern of grazing has not been studied to over larger scales to the same extent as it has been at small scales. Nor has the effect of community layout on grazing on the preferred community been much studied.

I investigated the effect of the layout of plant communities and herbivore density for grazing levels on a mosaic of heath and grassland communities. Grassland needs more grazing than the other communities to meet conservation management goals. It is also the plant community that is most preferred by the main herbivore (red deer). The effects of different levels of grazing are quite well known for heaths, but less well known for grasslands.

I experimentally reduced grazing on grassland to see how the effects varied within the grassland community. I found that the effects of reduced grazing and loss of grazing depended on grassland productivity and the starting plant species composition. Reducing grazing was beneficial for conservation goals on initially heavily grazed areas, but detrimental to goals on lightly grazed grasslands.

I analysed two datasets containing information on grazing impacts on grassland and heathlands over a large area (many km^2) to investigate the influence of the presence of the preferred plant community (grassland) and differences in local deer density on the distribution of grazing. I found that there was increased grazing on the heaths and bogs where grassland was abundant within 1km.

The effect on grassland was more complex. There was heavier grazing on grassland when there was a large area of grassland nearby, but lower grazing pressure was indicated when there was a large area of grassland further away. Deer density did not explain much of the variation in grazing levels, probably due to the coarse scale of the information on densities.

The increase in grazing on the less preferred community close to the preferred one at these larger scales means that the less preferred community is likely to become overgrazed in areas where a lot of grassland is present. Conservation management goals need to account for this and identify a suitable trade-off.

Abstract

Grazing is widely used as a tool in conservation management. Many plant communities of conservation importance are dependent on grazing for their existence, maintenance of species diversity and other valued characteristics. Plant community response to grazing depends on many factors, including site productivity and dominant plant species; setting appropriate grazing levels can therefore be challenging. The problems are magnified when more than one species or plant community is the target of conservation goals as they may need different levels of grazing. Where multiple plant communities are present in a mosaic, grazing pressure on the higher productivity community (usually the more attractive to herbivores) can affect the utilisation of the lower productivity communities: grazing on the less productive community is elevated in close proximity (a few metres) to the productive community. This increases the possibility of conflict in managing grazing for the conservation of both communities as low productivity communities can sustain only low levels of grazing. Less well studied are the effect of community layout at larger spatial scales (100s – 1000s of metres) and the effect of vegetation pattern on grazing on the productive community. It is also not well known how the spatial pattern of grazing is affected by changes in herbivore density.

I investigated the consequences of the spatial pattern of plant communities and changing herbivore density for grazing patterns on a complex multi-community mosaic and assessed the probable consequence for conservation of these plant communities. The plant mosaic comprised a mixture of species-rich grassland and several less productive communities, primarily heaths and bogs; the main grazers were red deer (*Cervus elaphus*). The grassland needs higher grazing levels than the others to meet management goals.

I used small scale experiments to investigate the effects of reducing grazing on grassland and how the effects varied within the grassland community. Elimination of grazing caused a rapid switch from short, herb-rich grassland towards a graminoid dominated, less diverse sward, as expected. The degree of change in diversity and herb cover was dependent on productivity. Experimental reduction in grazing had mixed consequences for grassland in relation to conservation goals due to pre-existing variation in intensity of grazing on the grassland. The condition of areas of initially heavily grazed and short vegetation improved, whilst taller grasslands deteriorated.

Analysis of large-scale datasets was used to investigate the influence of spatial pattern of community types and differences in large scale deer density on the distribution of grazing. There was increased grazing pressure on less productive plant communities where grassland was abundant within 1km and this was fairly consistent across communities and across different grazing indicators. There was an effect on grazing levels on grassland, but the explanatory power was generally lower and the effect less consistently present across indicators of grazing. Sward height and litter depth measures from one dataset indicated heavier grazing with more grassland present nearby (250m); however, lower grazing pressure was indicated by sward height and a combined grazing index when there was more grassland in a more distant zone (500-1000m). Deer density had limited power to explain large scale variation in impacts, probably due to the coarse scale of the information available and correlation with other variables. This limited the ability to thoroughly test the consequences of changes in deer density on the spatial pattern of impacts or investigate whether there was an interaction between deer density and spatial pattern.

The inherent conflict in conservation management of grazed communities of different productivities is increased by the influence of the spatial distribution of plant communities on the distribution of grazing; conservation management goals need to account for this and identify a suitable trade-off.

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Chapter 1: Introduction

1.1 Conservation management with grazing animals

Importance of herbivory to plant communities

Large herbivore grazing has a major influence on energy flow through an ecosystem as it determines how much primary productivity enters the animal part of the ecosystem and how much directly enters decomposition (Chapin III *et al*. 2002). In terrestrial ecosystems dominated by large herbivores the proportion of biomass consumed varies widely, largely dependent on the type of vegetation present. In forests, where much biomass is woody and indigestible, and much else out of reach of ground based herbivores, consumption is typically only 1-5% of net primary productivity (NPP). On grassland, where the allocation to defences and woody structural tissues is lower, consumption is higher; 25-50% consumption is common for rangeland and up to 90% is possible in intensively managed arable grassland (Vickery 1979, Chapin III *et al*. 2002).

Grazing has profound impacts on plant communities: it affects the species composition, spatial heterogeneity, nutrient cycling, species diversity and physical structure of the plant community (Hobbs & Huenneke 1992, Milchunas & Lauenroth 1993, Rosenthal *et al*. 2012). The presence of large herbivores can accelerate or retard successional processes, for example maintaining open communities and preventing succession to woodland (Jefferies *et al*. 1994) or accelerating succession to boreal forest by selective browsing on deciduous tree and shrub species, which allows unbrowsed spruce to become dominant (Prins 1998). In fire-dependent systems, herbivory can affect the fire regime, by removing flammable grass biomass, and herbivory interacts with soil fertility, rainfall and fire regime to determine the balance between open grassland and areas of trees or shrubs (Belsky 1992, Hobbs & Huenneke 1992, Scholes & Archer 1997). Soils are also affected by changes to nutrient cycling and physical compaction. All these processes alter habitat suitability for other animal groups, both above- and below-ground (e.g. Tscharntke & Greiler 1995, Dennis *et al*. 1997, Bardgett & Wardle 2003).

The effects of large herbivores are contingent upon the pre-existing biotic and abiotic conditions. The productivity of the plant community is an important determinant of plant community response to herbivory; in high productivity systems plant diversity is generally increased by light to moderate grazing as light is limiting and selective grazing on the dominant species reduces light competition and allows lower canopy species to coexist with the taller dominants (Hobbs 1996, Huisman & Olff 1998, Cingolani *et al*. 2005). Selective grazing can also increase structural heterogeneity by creating a variable sward structure which allows coexistence of more species (Hobbs 1996, Cid & Brizuela 1998). The lower the productivity, the less important light competition is and grazing can decrease diversity in this situation as it extirpates more species than it benefits (Milchunas *et al*. 1988, Huisman & Olff 1998, Huisman *et al*. 1999). This interaction of productivity and grazing on diversity has been found in practice across a broad range of grasslands (e.g. Milchunas & Lauenroth 1993, Jutila 1997, Bakker 1998, Bakker *et al*. 2006, Kohyani *et al*. 2008, Lezama *et al*. 2014), although there is much variation around the productivity value above which grazing increases diversity compared ungrazed grasslands (Bakker *et al*. 2006, Lezama *et al*. 2014).

This relationship between productivity, large herbivore grazing and diversity is modified by the evolutionary history of grazing in the area (Fig 1.1). Areas with a long history of grazing by large herbivores will tend to have more species in the regional pool that are adapted to grazing and therefore diversity in grazed grasslands is higher than ungrazed grasslands for a large range of grazing intensities, with highest diversity found at relatively high grazing levels (Fig 1.1). Conversely, areas with a short history of grazing have a smaller pool of species that can tolerate grazing, so the window of grazing intensity that increases diversity compared to ungrazed grassland will be much narrower (Cingolani *et al.* 2005).

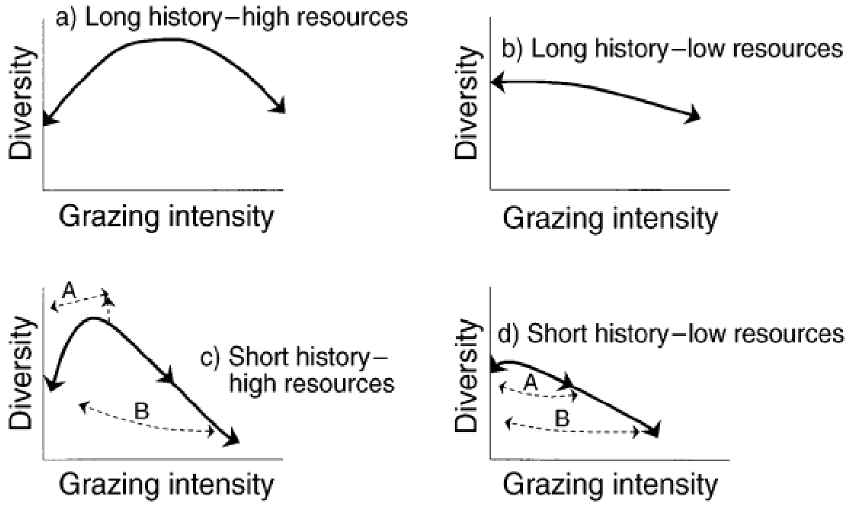

Fig 1.1: Typical curves for communities of four different combinations of grazing history and productivity. Source Cingolani *et al.* (2005) adapted from Milchunas *et al.* (1988). Dotted lines represent diversity trajectories once the system has entered an alternate stable state.

Differences in species of herbivore can also affect the outcome for the plant community (Bakker 1998, Bakker *et al.* 2006): different herbivores differ in their ability to be selective and in preferences for different types of plant material (e.g. browse or graze), due to underlying physiological differences (Gordon & Illius 1988, Hofmann 1989). The timing of grazing has also been shown to affect the response of at least some plant species and communities to grazing (e.g. Grant *et al.* 1978, Archer & Tieszen 1983, Hobbs & Huenneke 1992, Bullock *et al.* 2001, Marriott *et al.* 2004).

Selectivity and spatial patterns in grazing

Grazing is not uniform over space and time; herbivores graze selectively. An important aspect of diet selection is maximisation of food quality. This selection can be apparent as a very fine-scale process, as the animal selects the most palatable plants or plant parts (e.g. Duncan *et al.* 1994). As the temporal and spatial timescale of grazing increases, selection is governed by a greater number of factors making herbivore selection harder to predict. These include: the need to balance foraging time with other activities; predation pressure; the need to maintain a sufficient quantity of food intake; inter- and intra- specific competition; location of other important resources such as water and shelter (Senft *et al.* 1987, Bailey *et al.* 1996).

Small scale selection

Selective grazing within a plant community may occur because herbivores discriminate between different plant species. Their ability to do this will be limited by bite size; smaller herbivores are generally able to be more selective on fine grained swards (Gordon & Illius 1988). Alternatively, on grassland swards particularly, the dominant species may all be fairly palatable (or their spatial arrangement is too fine grained for animals to exert much selection on the basis of pre-existing variation in the sward) but herbivores can still create and maintain spatial heterogeneity from an initially homogeneous sward by selecting areas previously grazed and avoiding latrine areas (Cid & Brizuela 1998, Beecham *et al.* 1999, Dumont *et al.* 2012). A grazed area is maintained at a younger growth stage and is richer in nutrients and more digestible, so animals continue to select these areas, creating a positive feedback loop (McNaughton 1976, 1985). This results in the creation of heavily grazed 'lawns' alongside taller areas that are seldom grazed (Beecham *et al.* 1999). Up to 90% of the NPP can be consumed on these lawns (McNaughton 1985, Jefferies 1988), in contrast to the 25-50% average consumption on rangeland. Grazing lawn patterns are found to be relatively stable between years under some circumstances (Van Den Bos & Bakker 1990, Dumont *et al.* 2012). Creation of grazing lawns results in higher functional diversity of grassland than uniform heavy grazing or a uniform ungrazed sward. In the longer term this may lead to increased diversity of vegetation types in grazed and ungrazed patches (Adler *et al.* 2001). This grazing lawn effect will occur even on initially fairly uniform swards when grazing intensity is low, but at higher grazing intensities, where most of the area will be utilised, any grazing lawns and contrasting unused areas become distinct (e.g. Cid & Brizuela 1998).

It is also possible for grazing to homogenise vegetation. This occurs if there is a preference for less recently used vegetation, which can occur under several circumstances such as when regrowth is of insufficient quantity to meet the needs of herbivores or grazing causes a longer term shift to less palatable species in heavily grazed areas (Beecham *et al.* 1999, Adler *et al.* 2001).

Selective grazing on a multi-community mosaic

In multi-community mosaics, there will usually be a preference for one community over others; often the most productive is preferred, and this will induce variation in grazing intensity between communities. However, selection in this manner is rarely absolute and the less productive communities are also likely to be grazed to some extent, particularly when the preferred resource is depleted (Bailey *et al.* 1996, van Beest *et al.* 2010b). The spatial layout of plant communities is also important: an area of the preferred plant community can act as a focus for grazing in a similar way to a watering point and browsing on the less preferred community is increased when in proximity to the preferred one (e.g. Clarke *et al.* 1995b, Hester *et al.* 1996, Dumont *et al.* 2002). This effect is analogous to the well documented effect of elevated herbivore impact around a central attractive resource such as waterholes in arid rangelands and around supplementary feeding stations in northern hemisphere temperate and boreal forest (Pickup *et al*. 1998, Ball *et al*. 2000, Putman & Staines 2004, Mathisen *et al*. 2014). Increased utilisation of the less productive community in areas where the productive one is abundant is an example of the 'spill-over' effect predicted by Oksanen (1990): grazing on the less productive community is driven by the herbivore population supported by the productive community.

Heather-grass mosaics have frequently been used as a model system for the study of the influence of spatial pattern of communities on the spatial pattern of grazing. Grassland is the more attractive, productive community and is preferentially grazed (Clarke *et al.* 1995a, Milner *et al.* 2002), at least during the growing season; preference has been reported to reduce or reverse (Mitchell *et al.* 1977, Gordon 1989b, Perez-Barberia *et al.* 2013) over winter when availability and digestibility of the grass declines (Gordon 1989a, Armstrong *et al.* 1997, Perez-Barberia *et al.* 2013). Elevated grazing by deer and sheep has been demonstrated on heather within 0-5 m of the boundary between grass and heath (Clarke *et al.*, 1995b; Hester *et al.*, 1996; Oom & Hester, 1999). The characteristics of this 'edge effect' have been found to depend on grazing intensity and patch size (Hester & Baillie, 1998; Oom *et al.*, 2010). This edge effect has also been demonstrated on artificial grass swards of mixed species and in feeding experiments in which grazers consume more of the less preferred resource in proximity to the preferred one (Dumont *et al.* 2002, Wang *et al.* 2009).

In general, aggregation of the preferred resource into homogeneous patches facilitates selection at small scales as it decreases search time and the cost of turning to stay within a patch that is small compared to herbivore body size (Wallis De Vries *et al.* 1999, Dumont *et al.* 2002, Cromsigt & Olff 2008). This effect is found in multiple grazer systems at a scale of 1- a few 10s m. Other than this, there have been fewer studies that examine the role of spatial layout of the vegetation on the grazing on the preferred community. A modelling study suggested that the preferred resource also ought to be affected, being less used in areas where the less preferred resource is abundant (Oom *et al.* 2008). A paddock-scale feeding experiment supported this prediction (Wang *et al.* 2009). This effect of increased grazing in proximity to the preferred community and decreased grazing in areas of mainly poor quality resources is also analogous to associational susceptibility or resistance widely found in large mammal herbivory on trees (Barbosa *et al.* 2009).

Fewer studies have explored how the spatial layout of resources at larger scale influences grazing patterns. However, Palmer *et al.* (2003) found higher levels of browsing on the edge of patches of heather in 0.25 km^2 areas where grassland was abundant compared with areas with little grassland, and Speed *et al.* (2009) found increased utilisation of both preferred and less preferred communities when there was more of the preferred resource within 500m.

There is evidence from several studies that food quality is one influence on ungulates' selection of broad areas within the home range, which presumably impacts grazing and browsing levels on both preferred and less preferred food resources at smaller scales: moose have been found to select areas of their home range where there are a higher proportion of preferred food resources (Månsson *et al.* 2007, van Beest *et al.* 2010b). However, this must be balanced with the quantity of food; moose switch from using high quality areas of their home range to areas with lower abundance of high quality forage but an abundance of poorer quality forage in late winter, presumable in response to resource depletion in high quality areas (van Beest *et al.* 2010b). Not all studies of this type show a clear effect of productivity on habitat use: the effect of habitat productivity on browsing levels by red deer on three browse species was inconsistent and non-linear (Mysterud *et al.* 2010).

Herbivore grazing and conservation

Whether the effects of herbivory on plant communities and their associated fauna is positive or negative in terms of fulfilling conservation goals is dependent on the plant community in question and the timing and intensity of grazing (Hobbs & Huenneke 1992).

Annex 1 of the European Habitats Directive lists 201 terrestrial habitats which are of conservation value (Council of the European Communities 1992). A recent study found that the existence of 63 of these was wholly or partially dependent on agricultural activity, mainly mowing or grazing activity, and a further 23 are dependent in part of their range

(Halada *et al*. 2011). These habitats included a range of plant communities, mainly grasslands, but also salt marshes, dwarf shrub heath and wooded grassland communities.

Generally, light to moderate grazing is considered beneficial to these communities, increasing plant species and structural diversity, which will encourage a diversity of dependent fauna, but heavy grazing can still be detrimental to these communities (e.g. Thompson *et al*. 1995, Tscharntke & Greiler 1995, Bakker 1998, Dennis *et al*. 2002, Dennis *et al*. 2008). What constitutes "moderate" and appropriate grazing will depend firstly on management goals and secondly on the plant community response, which will depend on the tolerance of plants for grazing, species of grazer and the productivity of the site, among other factors (Mysterud 2006, Ebrahimi *et al.* 2010).

Grazing that is heavier than can be sustained by a plant community in the long-term without a change in characteristics of the plant community or soils, and which is considered detrimental, is often referred to as 'overgrazing'. The converse situation, where very light or no grazing causes undesirable changes, may be referred to as 'under-grazing'. These terms will be used throughout this thesis; however it is important to remember that these are subjective terms that can only be defined with reference to particular management goals (Gordon *et al.* 2004, Mysterud 2006). Overgrazing is commonly used in the livestock industry to mean a level of grazing that causes a long-term decline in vegetation productivity or shift in vegetation type leading to decline in the ability of rangeland to produce livestock (Wilson & Macleod 1991), but this definition in insufficient to define overgrazing in conservation terms. With reference to conservation goals, 'under-' or 'over- grazing' may occur when, for example: extirpation of a valued species occurs; or there is a reduction in diversity; or when grazing, or its absence, causes a shift in the type of plant community away from the one desired.

Although all the plant communities listed by Halada *et al.* (2011) are expected to benefit from some grazing, it is known that they require different levels of grazing. Dwarf-shrub communities will usually tolerate less grazing than grassland before they become overgrazed, as dwarf-shrubs are less tolerant of heavy defoliation and trampling than most grasses (Thompson *et al.* 1995).

Both abandonment of agricultural activity and (over-)grazing are listed as threats to many of these grazing-dependent communities in the most recent pan-European assessment of Annex 1 habitats (European Environment Agency 2008). Abandonment of farmland in Europe in recent decades has been higher in areas of high farmland biodiversity than other areas and this trend is predicted to continue (Bignal & McCracken

1996, McCracken & Huband 2005, Renwick *et al.* 2013). There is particular concern over abandonment of grasslands, as high nature value grasslands in EU countries are almost exclusively present as grazed rangelands and these are particularly likely to deteriorate in response to reduced grazing pressure (Bignal & McCracken 1996, McCracken & Huband 2005, Rural Policy Centre 2008). Where grazing has continued however, there are reports of overgrazing on several communities listed by Halada *et al.* (2011), especially affecting heaths, but also grasslands (e.g. Petit & Elbersen 2006, JNCC 2007).

Consideration of grazers in conservation management also extends to wild herbivores: in many areas of NW Europe and North America large wild herbivores are on the increase, generating concern about overgrazing (Gordon *et al.* 2004, Milner *et al.* 2006, Mysterud 2006). However, in areas where grazing of domestic stock has been abandoned, increasing numbers of wild herbivores can be beneficial to plant communities, functionally replacing domestic stock and maintaining valued communities created under agriculture (e.g. Schutz *et al.* 2003). However, it cannot be assumed that wild herbivores will have identical effects to domestic stock that they replace. In fact it is unlikely; different species have different selective preferences and wild herbivores unlike domestic stock are not generally confined by fences or fed over winter, this will result in different patterns of grazing and different impacts on the vegetation (Hope *et al.* 1996). Winter feeding of stock allows relatively higher densities of herbivores than are reached by wild herbivores limited by food resources in winter.

Managing grazing for conservation

Determining the optimal level of grazing at a site first requires the setting of specific management goals (Mysterud 2006). The simplest situation is if a site is important for one specific species or plant community. Even then, the slow responses of some plant communities make it difficult to study long term effects of different grazing regimes, and the long- and short-term effects of grazing can differ (Jefferies *et al.* 1994, Dumont *et al.* 2011). There is also a relative paucity of studies comparing varying levels of grazing compared to those comparing presence/absence of grazing. The level of impact on the community which can be sustained is well known for some communities - for example the proportion of offtake that *Calluna vulgaris* heath can sustain before the dominant species begins to decline is well characterised (Pakeman & Nolan 2009) - but this is unusual.

Often nature conservation areas aim to benefit multiple species or assemblages of species, and this can cause conflicts in management: even where all goals require some grazing, optimising grazing regime for one species or group of species won't necessarily benefit other groups or species and compromise will be necessary. For example, grazing levels calculated to optimise plant diversity on species-rich grassland will not necessarily promote diversity of the associated insect fauna (Wallis De Vries *et al.* 2002, van Teeffelen *et al.* 2008).

Where a site has multiple plant assemblages with different grazing requirements, the likelihood of conflict depends on the relative attractiveness (to herbivores) and accessibility of the plant communities. There is obvious conflict where both communities are equally accessible and attractive and one needs a higher level of grazing to be maintained than the other can tolerate (or where the less tolerant community is more attractive or accessible to herbivores) and management to benefit both communities would need to involve fencing or strict herding of animals. Where the less tolerant community is also less attractive, or is less accessible, a grazing regime to favour both may be possible (Holland *et al*. 2010). However, where communities are adjacent, the spill-over effect identified by Oksanen (1990) and studied in heather-grass mosaics (see previous section), increases the potential for conflict. In order to protect the less productive community, the grazing level may have to be reduced further than a prescription based upon simple calculations that do not take this effect into account (Palmer *et al.* 2004). The prescribed reduction in grazing to protect the less productive community would then result in under-grazing of the more productive community.

Given the extent and strength of large herbivore impacts on ecosystems, understanding the causes and consequences of spatial patterns in grazing is of present concern to conservation interests, livestock managers and forestry management alike (Gordon *et al.* 2004, Bailey & Provenza 2008). This thesis contributes to the understanding of spatial patterns in grazing impacts determined by animal behaviour and plant response.

1.2 Research questions and thesis outline

Research questions

In the research described in this thesis I aimed to answer three main questions.

The likely response of the productive community in response to reduced grazing to protect a nearby vulnerable community is of interest when managing a multi-community mosaic, as are factors that may induce variation in response to reduced grazing and the likely reversibility of the negative consequences of a short period of under-grazing. Although general rules about how grassland responds to grazing are known, given the number of variables that influence response to grazing (see section 1.1), it is not possible to predict the optimal level of grazing for a site *a priori*. Also, the range of grazing pressures that will fulfil site goals to an acceptable standard may be known roughly but not precisely. The first question addressed in the thesis is: what are the short-term consequences for species-rich grassland in a multi-community mosaic when grazing is reduced or removed to protect other communities? And how does plant community response vary depending on initial conditions of grazing intensity and productivity?

The second broad research question addresses two areas where there are gaps in the literature in the knowledge about how the spatial distribution of plant communities controls the spatial distribution of herbivory. As discussed in section 1.1 , above, there has been little research on large herbivores on large scale mosaics (at the scale of home range size or above) that addresses this question directly. Further, the emphasis in studies on the model heather grass mosaic system has generally been on the pattern of grazing on the less preferred community (*Calluna*), and the preferred community is rarely considered. Field studies in forestry, where selection operates at the scale of individual trees, and mechanistic, small scale modelling of heather-grass mosaics, suggest that an effect of community layout on herbivory on the preferred community is possible, even likely. I therefore wanted to investigate whether the preferred vegetation community is also affected by the spatial layout of vegetation communities. The second question addressed in the thesis is this: to what extent does the distribution of plant communities at the landscape scale (100s m^2 to 1000s m^2) explain small scale grazing impacts on both the preferred and less preferred communities? And secondarily, how does this interact with herbivore density?

As the research is motivated by problems in conservation management, especially the potential conflict in management of multiple plant communities, there is a third, adjunct question to be answered: what implications do the answers to questions 1 and 2 have for conservation management?

Outline of thesis

Broadly, the thesis is in two parts: the first research question (the effects of grazing reduction and exclusion on grassland) is addressed through two small scale experimental studies. One excluded grazing for a period of six months (over the growing season) and for three years on several areas of short grassland, differing in initial species composition and productivity; the other used a novel method of reducing grazing on short and tall grasslands for a period of just over two years. These are detailed in Chapter 2 and Chapter 3, respectively.

The second research question is addressed through analysis of previously collected data recording direct and indirect measures of grazing on a variety of plant communities. In Chapter 4, a dataset collected as part of a larger restoration project on a substantial scale and at multiple time-points was analysed to assess the control of grazing impacts by plant community spatial distribution and deer density. In Chapter 5, a similar approach was used in the analysis of data collected specifically to assess the grazing impact on, and condition in relation to conservation goals of, several plant communities at a single time point on the same geographical area.

The implications for conservation (third research question) are addressed throughout, as part of the discussion sections of Chapters 2-5. In particular, a section at the end of Chapter 3 (Sub-Chapter 3b) specifically relates the results of a reduced grazing experiment to criteria used to assess the conservation status of such grassland. Answering this research question also forms a major part of the general discussion in Chapter 6 where the broad implications and recommendations for conservation managers following from this research are discussed.

1.3 A case study of the conservation significance of the spatial distribution of grazing impacts at varying scales in a heterogeneous environment

Conservation importance and suitability as a study site

As established in section 1.1, understanding plant community response to grazing and the influences on the spatial pattern of grazing is important to conservation managers for several reasons. Many areas of conservation interest are managed by grazing. Understanding how herbivores use a heterogeneous environment allows potential conflicts in management to be identified in advance, realistic conservation goals to be set in light of this, and a grazing regime designed to achieve these goals.

The case study presented in this thesis is the Island of Rum, which is one of the islands of the Inner Hebrides located off the west coast of Scotland at 57° 0'N 6°20'W (Fig 1.2).

The island was considered suitable as a study site for several reasons:

- Vegetation communities with contrasting grazing requirements are present in a complex mosaic.
- Herbivory is likely the primary influence on vegetation condition and change, as there is little other human activity on the island.
- The herbivore community is relatively simple, dominated by red deer (*Cervus elaphus*).
- Rum has been the subject of biological and ecological studies since the establishment of the National Nature Reserve (NNR) in 1957. Therefore there is good pre-existing background information on the ecology and biology of the flora and fauna. This is especially true of the ecology of the deer population, and to some extent of the vegetation communities.
- There is also ongoing monitoring and recording of the deer and plant communities, providing suitable datasets for use in analysis that cover the whole island area: covering a far greater extent (in time as well as space) than would be possible to collect in the time available for a PhD thesis.
- Finally, the island is a nationally and internationally important site for conservation. It contains 18 Annex I habitats and two Annex II species. It is also a Special Protection Area due to its breeding seabird assemblage and other protected bird species. Rum has the following national and international designations of conservation importance:

- National Nature reserve (NNR),
- National Scenic area (NSA),
- Special Area of Conservation (SAC),
- Special Protection Area (SPA),
- Site of Special Scientific Interest (SSSI),
- NATURA 2000 site (SNH 2009).

Climate and vegetation

Rum has a mild oceanic climate, with rainfall varying between 1500mm yr^{-1} in coastal areas and >3000 mm yr^{-1} in the mountainous south west of the island (Clutton-Brock & Ball 1987). The present-day vegetation is typical of the west coast Scottish vegetation in upland and uncultivated areas: the main vegetation types are wet heath and blanket bog; *Molinia caerulea* is frequently a dominant or co-dominant species on the wet heaths. Smaller areas of dry and herb-rich heaths are also present on well drained soils, often in mosaics with grassland (Pearman *et al.* 2008). Montane heaths, containing a rich flora of oceanic bryophytes, are more widespread on summits and exposed ridges. Various types of grasslands are present, primarily in coastal and upland areas, these include calaminarian grassland on ultrabasic substrate in the uplands; unproductive, *Nardus*-dominated grassland grading into more productive species-poor and species-rich *Agrostis-Festuca* grassland on both acid and calcareous substrate (Bates *et al.* 2002, Pearman *et al.* 2008). 'Calcareous' forms of *Agrostis-Festuca* grassland are restricted to limestone outcrops and areas of base rich rocks in the Rum Cuillin (the mountains in the south-east of the island). In places where the influence of basic bedrock becomes low they grade into acid grasslands (Pearman *et al.* 2008). Acid *Agrostis-Festuca* grassland is more widespread, on free draining soils overlying siliceous rock, and where the dominance of shrubs and more competitive grasses has been reduced by grazing. They are also found in areas of former agricultural improvement and in nutrient rich soils around the breeding burrows of Manx shearwaters in the Rum Cuillin. There are restricted areas of montane grassland and grass heaths in fragmentary stands higher in the Cullins. Maritime grassland occurs on coastal areas and clifftops, replaced by *Pteridium aquilinum* dominated communities in ungrazed areas (Bates *et al.* 2002, Pearman *et al.* 2008). Specialist plant communities of acid and calcareous rocks and scree are present in mountain areas. Small blocks of planted mixed native woodland are present, all originally fenced (see Fig 1.4) (Bates *et al.* 2002, Pearman *et al.* 2008).

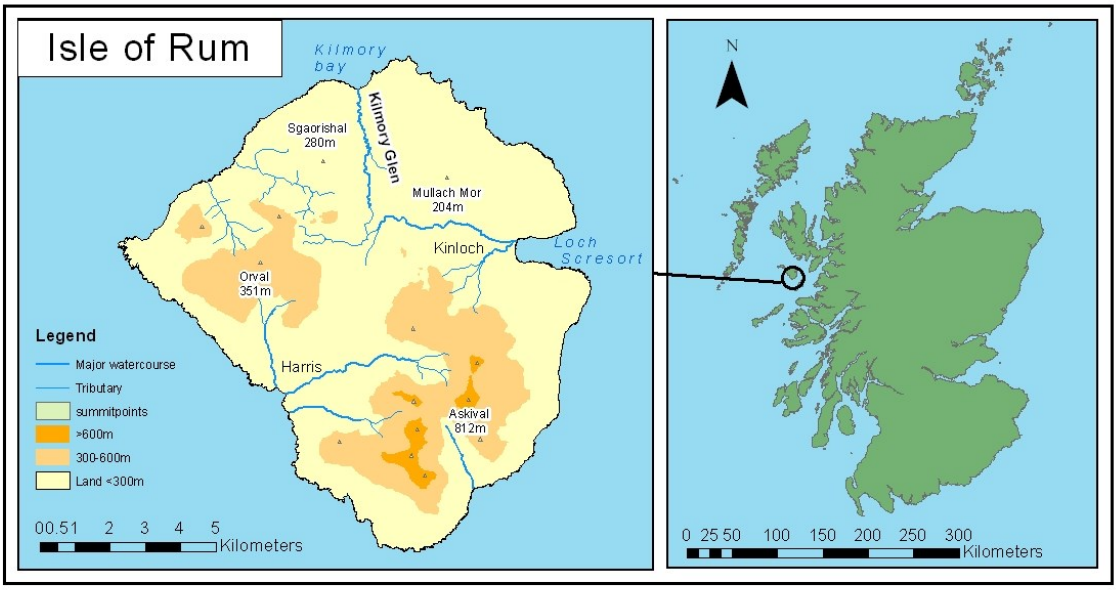

Fig 1.2: Location map of Rum, derived from OS survey data. © Crown Copyright and Database Right [2014]. Ordnance Survey (Digimap Licence).

Grazing and vegetation history

In common with much of the Scottish Highlands (Thompson & Brown 1992), the Isle of Rum has a long history of human occupation and livestock grazing, extending from the Neolithic period until the present day (Love 1981, Lowe 1998). Subsistence agriculture was practised from early human occupation until 1826, when the original inhabitants were cleared to make way for sheep farming. There is no record of when or how red deer originally came to the island, but they were known to be common by the 16th century. They were hunted to extinction on the island at the end of the 18th century, but reintroduced for the purpose of hunting around 1845. Numbers had risen to circa. 800 by the end of the 19th century, and to 1200 by 1939; in 1957, 1,584 deer were counted (Eggeling 1964, Clutton-Brock 1999, Pearman *et al.* 2008). Between 1845 and 1957, the island was managed for sheep grazing (with a variable number of sheep, commonly in excess of 3,000 and up to 8,000) and as a sporting estate for deer and to a lesser extent, grouse, with associated heather burning (Eggeling 1964, Pearman *et al.* 2008).

The prehistory of the vegetation on the island has been the subject of only limited study, but it appears to mirror the general Scottish pattern: a post-glaciation colonisation phase from 12000- 8000BP; woodland reaching a maximum at 5000-4000BP; followed by a steep decline in wooded area and an increase in area of peat bog (Hirons & Edwards 1990, Lowe 1998, Ashmole 2006). The woodland on Rum was probably fairly open and dominated by hazel and aspen, and there is evidence that substantial areas of open heath and grassland communities persisted during this period on exposed and higher altitude sites unsuitable for tree growth (Hirons & Edwards 1990, Lowe 1998). Lowe (1998) tends to interpret the decline in woodland as driven by anthropogenic burning and clearance for agriculture; this is supported by an increase in charcoal and pollen from cultivated species in a peat core taken from Kinloch Glen from around 3000 BP (Hirons & Edwards 1990). Wood (2000) argues that the pattern of plant species changes found in the pollen record indicate that the arrival of large herbivores (whether wild or domestic) was the main factor, causing loss of tree cover by inhibiting regeneration. Whichever interpretation is correct, the present day plant communities originated and have persisted under a long history grazing by both wild and domesticated herbivores.

Grasslands in glen (valley) bottoms and coastal grasslands in particular have been affected by other forms of management activity during the period of subsistence agriculture, such as rotational cropping and some improvement by additions of seaweed fertiliser and/or drainage (Eggeling 1964, Clutton-Brock & Ball 1987). These grasslands have been shown to be dependent on grazing to persist in their species-rich form. Grazing exclusion leads rapidly (within five years) to species loss, mainly of low growing herb species (Ball 1974, Unpublished). Remaining species and colonisers were mainly taller grasses and ericoid shrubs; after 12-25 years, the community had changed to a species-poor grassland, with heath elements in places, and there is an accumulation of dead biomass (Virtanen *et al.* 2002, Ball 1998, unpublished). Species-rich grassland and herb-rich heath are in theory interchangeable on richer soils depending on grazing levels (Miles 1966) in the same way that on poorer soils dry heath can give way to a species-poor grassland under heavy grazing (Alonso & Hartley 1998). However, after 35 years of experimental grazing exclusion on the Rum grasslands, grasses still dominated exclusion plots that were placed on species-rich and species-poor *Agrostis-Festuca* grasslands in 1957 (Ball 1998, Unpublished), which suggests that replacement of grassland with heath in these areas is a slow process taking many decades, if it occurs at all. This may be because once tall competitive grasses have become dominant, some form of disruption to the grass and litter layer is usually required to allow *Calluna* to re-establish (this may be supplied by light grazing and associated trampling) (Bokdam 2001, Marrs *et al.* 2004, Milligan *et al.* 2004, Mitchell *et al.* 2008). In the total absence of grazing or other deliberate disturbance as part of land management activities, this may only occur following accidental fire or other abiotic disturbance. For the same reason, conversion of grasslands to scrub or woodland following grazing cessation is only likely if a there is a seed source in proximity, and species can establish before the grass canopy and litter layer build up, inhibiting seedling establishment and development (Gong *et al.* 1991, Scott *et al.* 2000). After 35 years, only one exclusion plot was reported to contain any woodland species, and this plot had only one individual rowan (*Sorbus aucuparia*) and bluebell (*Hyacinthoides non-scripta*) (Ball 1998, Unpublished). Over 50 years after establishment of the exclusion plots, only one remains intact on grasslands and this only has one woody tree species, rowan, which is represented by a single individual. Some coastal grasslands within the deer fence around Kinloch in the east of the island (Fig 1.2) have become dominated by *Pteridium aquilinum* (which can invade rapidly and vegetatively) since the fence was established (Pearman *et al.* 2008).

Influences on vegetation 1957 – present

In 1957, the island became a nature reserve, and sheep grazing was discontinued (1,750 sheep were removed from the island in 1957) (Eggeling 1964, Clutton-Brock 1999), as was burning of heather for grouse management. The main influence on the vegetation from 1957 up to the present has been the deer population (numbers from 1957 to present given in Fig 1.3). The other remaining herbivores are approximately 350 feral goats, a herd of around 20 ponies and a herd of 40 Highland cattle allowed to roam freely (Pearman *et al*. 2008). There are no rabbits, hares or voles on the island.

Vegetation monitoring on several communities from 1957 to 1993 found a number of floristic changes that following the cessation of muir-burn and the removal of sheep and cattle in 1957. On wet heath, fen and herb rich heaths this was marked by a decline in dwarf shrubs and an increase in the grasses present, possibly due to cessation of burning and remaining grazing pressure causing an opening of the canopy allowing grasses to increase (Ball 1974). Species-poor *Agrostis-Festuca* grasslands and herb-rich heaths also showed a decline in some small herb species typical of heavily grazed grassland and a corresponding increase in locally present, competitive species. (Ball 1974, Ball & Hirst 1994, Unpublished, Ball Unpublished). Changes on species-rich *Agrostis-Festuca* grasslands were much smaller: fewer species declined, and declines were slower, probably because these were the community types most heavily selected by deer and therefore were still heavily grazed (Ball 1974; Gordon 1989a).

In the area where cattle were reintroduced in 1972, several small herb species had recolonized or increased in abundance 20 years after the reintroduction of cattle, at the expense of taller herbs and grasses (Ball & Hirst, 1994, Unpublished). Grassland at

Kilmory (where the deer population increased following cessation of culling in 1972) also gained small herb species over the same time period, so the effects of reintroduction of cattle were probably due to the increase in total grazing pressure rather than introduction of a different species of grazer (Ball, Unpublished). Similarly, in 2002, flowering rates were found to be higher on grassland with cattle present than in areas with no cattle, but flowering rates were also higher in areas with an unculled deer population than in areas with a culled population (Virtanen *et al.* 2002), which again suggests that the higher grazing pressure *pre-se* encouraged small herb flowering, and perhaps the species of grazer was less important. Re-introduction of cattle caused unique changes to wet communities however, which are not replicated in areas of unculled deer population; species numbers increased in these communities but there was a decrease in the differentiation between marsh, fen and bog communities (Ball & Hirst, 1994, Unpublished).

No wholesale changes in community type were reported by Ball (1974, 1994, 1998 Unpublished) in response to the changes in grazing pressure over the time period from 1957 (cessation of sheep grazing) through to 1998, covering in the reintroduction of cattle in 1972 and the changes in deer population (net decline in numbers, notably in the 1990s, see Fig 1.3, but a rising population in the north block following cessation of culling in 1972). The earliest detailed information about the distribution of vegetation types is from a detailed vegetation map of the whole island produced from aerial photos taken in 1964 and subsequent ground surveys (Ferreira 1970), when presumably the vegetation was still recovering from heavy sheep grazing. Although a detailed comparison is restricted by the differences in the way vegetation communities are recorded and categorised, a comparison of this map (Ferreira 1970) with one produced by survey in 1998 (Bates *et al*. 2002), thus covering a similar time period to Ball (1974, 1994, 1998 Unpublished) Ball & Hirst (1994), also suggests that no wholesale replacement of broad community types over this period. However, there is some net loss of *Agrostis-Festuca* grassland, the most sensitive of the communities to changes in grazing pressure (species rich and species poor *Agrostis-Festuca* grasslands are not differentiated on the older map) (Ferreira 1970, Bates *et al*. 2002). The largest areas of grasslands, (coastal areas in Glen Harris, Kilmory Glen and in upland areas on Fionchra, Orval and in the Rum Cuillin) remain and have approximately the same areal extent. The grassland at Harris may even have expanded slightly. Elsewhere, small areas of *Agrostis-Festuca* grassland have been lost, to be replaced primarily by *Molinia* meadow in low-lying areas, and by dry heaths, either

Calluna dominated or more species-rich heaths, in upland areas (see Appendix I for maps and details).

Red deer numbers have been reduced in recent decades by culling, particularly between 1992 and 2000 when some areas were culled heavily in an attempt to manipulate the sex ratio (Clutton-Brock *et al.* 2002a). Changes to the sex ratio of deer appeared to have only slight effects on the selection of plant communities by deer (Clutton-Brock *et al.* 2002a) only the more productive *Agrostis-Festuca* grasslands were affected in terms of species composition (Virtanen *et al.* 2002). In areas where hinds were most heavily culled, small herbs had lower cover and *Festuca rubra* was more dominant (Virtanen *et al.* 2002). It is believed that goat numbers have increased following decline in deer numbers, partially replacing the grazing pressure lost due to higher deer culls: there is also observational evidence that goats are increasing their range to areas of the island where they were not seen previously. Census data for goats is sparse in recent years, but a count in 2010 found 349 individuals, whereas regular censuses in the 1960s-1970s found the population cycling between approximately 100 and 180 animals (Boyd 1981). The cattle herd mainly reside in Glen Harris while the ponies roam between Glen Harris and Kilmory Glen (Fig 1.2).

The recent trend of warming climate and changes in precipitation have led to an increase in productivity of species-rich grassland, especially in an earlier onset of spring growth and greater productivity in autumn, although there is much inter-annual variation (Bento 2012). Climatic variation affects population dynamics of the deer in the northern, un-culled part of the island, but numbers in most of the island are controlled by culling (Albon *et al.* 1983, Langvatn *et al.* 1996). There has been some suggestion that climatic variation and consequent changes in productivity of grassland could have altered herbivore grazing behaviour in the culled part of the island: an increase in selection for grasslands in the period 1992-2002 compared with the previous decade was noted and a climatic link suggested but not empirically tested (Clutton-Brock *et al.* 2002a).

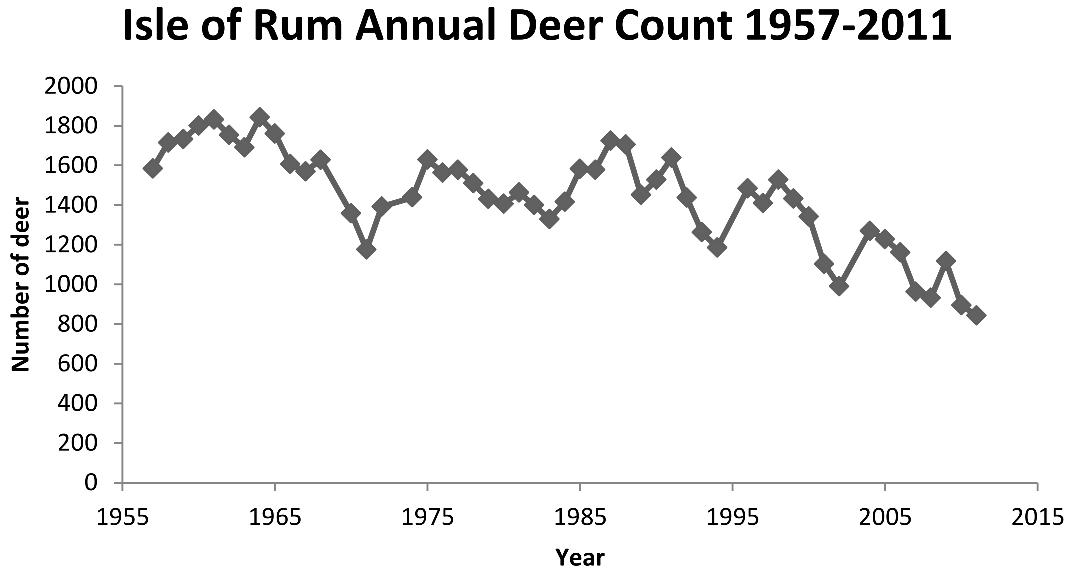

Fig 1.3: Deer numbers since 1957 on Rum. Numbers from the annual census carried out by the Deer Commission for Scotland (DCS). Counts carried out on foot from 1957-2002, helicopter counts 2002-present.

Annex 1 plant communities: conservation status

The entire island is a national nature reserve (NNR) owned by Scottish Natural Heritage (SNH). Thirteen terrestrial plant communities listed in Annex 1 of the European Habitats Directive are present, covering 72.2% of the reserve area. These include several types of heath, blanket bogs, grasslands and vegetation of rocky slopes and screes, (full list in Table 1.1) (Council of the European Communities 1992, McLeod *et al.* 2009, JNCC 2011). Of these, wet heath covers the largest area (c. 30% of the reserve area) followed by blanket bog (13.4%), dry heath (8.3%), and grasslands (5.9%) (JNCC 2011). Other protected communities occupy <3% of the area each (Fig 1.4). As a conservation organisation, SNH aim to manage the site in such a way that all the plant communities are in a ‘favourable’ condition, as defined in the European Habitats Directive 1992, that is:

> *“its natural range and areas it covers within that range are stable or increasing, and the specific structure and functions which are necessary for its long-term maintenance exist and are likely to continue to exist for the foreseeable future, and the conservation status of its typical species is favourable”* (Council of the European Communities 1992).

The designated plant communities on Rum, which are typical of North West Scotland, have very different grazing requirements (Table 1.1). The greatest potential for conflict is between species-rich *Nardus* grasslands and most other Annex 1 communities present. These grasslands require more grazing than the other habitats and are vulnerable to too little grazing. Most other habitats present can only sustain much lower levels of grazing (Holland *et al.* 2010). Inaccessible areas of tall herbs and scree/rocky slope communities are likely an exception to this pattern as they may be protected from herbivory by their location.

On Rum, as elsewhere, the grasslands are selected more heavily than any other community for grazing (Charles *et al.* 1977, Gordon 1989b), which potentially mitigates this conflict; however, conflict in management is still evident. Three recent studies commissioned by SNH suggest that overgrazing is a problem on wet, dry, alpine and boreal heaths and of blanket bog, although there is much variation around the island in the proportion of surveyed sites found to be over-grazed (Dayton 2008, Britton & Pakeman 2009, Dayton 2011). These three reports gave slightly conflicting reports on the appropriateness of grazing levels on species-rich grassland: one assessment found 2.4% to be over-grazed and 13.7% of surveyed sites to be under-grazed (Dayton 2008), but of the small number of grasslands sites surveyed in a follow-up survey more sites were found to be overgrazed than under-grazed (Dayton 2011). A seven-year study by Britton & Pakeman (2009) concluded that declining grazing over the time period 2001-2008 was then threatening grasslands with under-grazing: the main evidence for this being the build-up of a litter layer on 76% of grassland plots by 2008.

In short, conflict in management is evident, with some overgrazing on the less productive communities and evidence of mainly under-grazing affecting the more productive species-rich grassland. There is also variation in the levels of grazing impact around the island. This makes it a good field site for the study of plant-herbivore dynamics on a complex vegetation mosaic, and the problem of managing multiple vegetation communities with free-ranging herbivores.

Table 1.1: List of terrestrial plant communities ('features') present on the Isle of Rum and protected under Annex 1 of the EU Habitat Directive. Rum contains particularly good examples of eight of these habitat types and these were the main reasons for Rum's designation as a Special Area of Conservation (SAC). The vulnerability of each habitat type to decline in condition due to higher or lower than optimal grazing levels is shown. Data derived from JNCC (2011, 2013b) and (Holland *et al.* 2010). Grey blocks indicate information not available.

Habitat	Primary reason for selection of Rum as an SAC?	Vulnerability to under-grazing	Vulnerability to over-grazing
Northern Atlantic wet heaths with *Erica tetralix*	Yes	Low	Medium
European dry heaths	Yes	Low to medium	Low to medium
Calaminarian grasslands of the *Violetalia calaminariae*	Yes	Low to medium	Low to medium
Species-rich *Nardus stricta* grassland, on siliceous substrates in mountain areas*	Yes	High	Low
Calcareous and calcshist screes of the montane to alpine levels	Yes	Low	Medium
Vegetated sea cliffs of the Atlantic and Baltic coasts	Yes	Low	Medium
Alpine and Boreal heaths	Yes	Low	Medium
Hydrophilous tall herb fringe communities of plains and of montane to alpine levels	Yes	None	High
Blanket bogs	No	Low	Medium
Depressions on peat substrates of the *Rhynchosporion*	No	▨	▨
Alkaline fens	No	Low	Medium
Siliceous scree of the montane to snow levels	No	None	High
Calcareous rocky slopes with chasmophytic vegetation	No	Low	Medium
Siliceous rocky slopes with chasmophytic vegetation	No	▨	▨

* This is not the typical species poor acid grassland dominated by *Nardus* often found in upland areas (U5 *Nardus stricta-Galium saxatile* community and subtypes in the National Vegetation Classification (NVC)). In the UK, 'Species-rich *Nardus stricta* grassland' is something of a misnomer as it corresponds most closely to the species composition of grassland types: CG10 (*Festuca ovina – Agrostis capillaris – Thymus praecox* grassland) and CG11 (*Festuca ovina – Agrostis capillaris – Alchemilla alpina* grassland), where these are found on siliceous substrate. *Nardus* is usually present in the sward but *Festuca* and *Agrostis* spps. are the dominant grasses. More species-rich sub-types of NVC communities U4 (*Festuca ovina – Agrostis capillaris – Galium saxatile* grassland) are also included within the habitat definition, as is the species-rich U5c sub-community (*Carex panicea – Viola riviniana* grassland) (Rodwell 1992, JNCC 2012b).

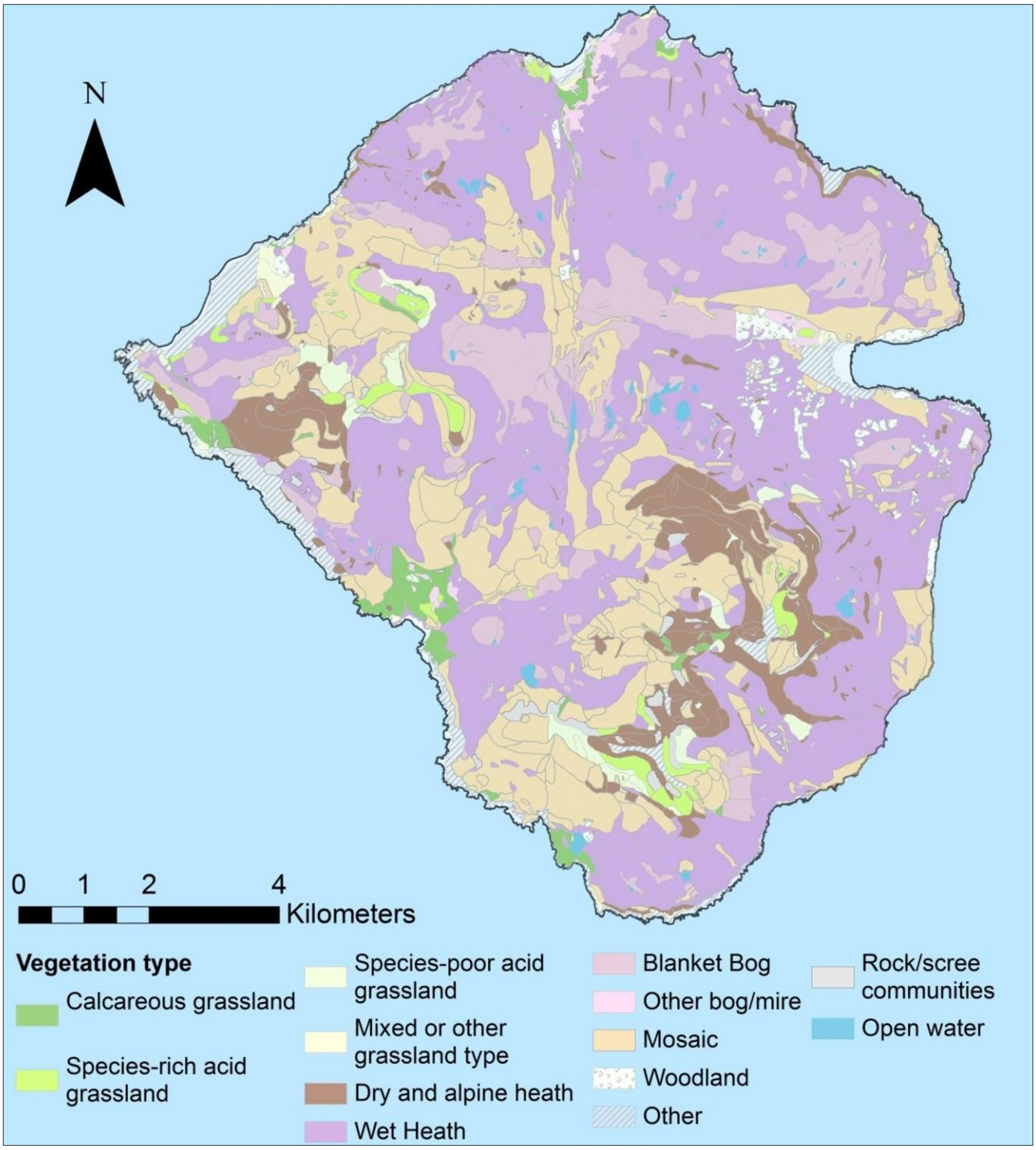

Fig 1.4: Map showing broad vegetation types on the Isle of Rum, based on a survey by Bates *et al.* (2002).

Box 1: Summary of research questions and thesis outline

Research question 1: What is the short term impact of reduction and exclusion of grazing on species rich grasslands and how does this very depending on initial conditions?

This was addressed through two small scale experimental studies, one excluding grazing for a period of six months (over the growing season) and for three years on several areas of short grassland, differing in initial species composition and productivity; the other used a novel method of reducing grazing on short and tall grasslands for a period of just over two years. These are detailed in Chapter 2 and Chapter 3, respectively.

Research question 2: To what extent can the distribution of plant communities at the landscape scale (100s m^2 to 1000 m^2) explain small scale grazing impacts on preferred and less preferred communities? How does this interact with deer density?

This was addressed through analysis of previously collected data recording direct and indirect measures of grazing on a variety of plant communities. In Chapter 4, a dataset collected as part of a larger restoration project over the entire island and at multiple time-points was analysed to assess the control of grazing impacts by plant community spatial distribution and deer density. In Chapter 5, a similar approach was used in the analysis of data collected specifically to assess the grazing impact on, and condition of, several plant communities at a single time point.

Research question 3: What are the implications of the answers to questions 1 and 2 for conservation managers?

This is addressed throughout in the discussion and conclusion sections of Chapters 2-5. In particular, Sub-Chapter 3b specifically addresses relates the results of a reduced grazing experiment to criteria used to assess the conservation status of such grassland. Answering this research question also forms a major part of the general discussion in Chapter 6 where the broad implications and recommendations for conservation managers following from this research are discussed.

Chapter 2: Response of species-rich grassland to the exclusion of grazing

2.1 Summary

- Many species-rich grasslands of conservation value are currently threatened by abandonment of grazing. Grazing reduction on grassland may also occur due to reduction of grazing to protect other, more grazing-sensitive communities of conservation importance.
- A short period of grazing reduction on species-rich grassland can sometimes benefit conservation goals by increasing vegetative spread and flowering of herbs species.
- I analysed the impact of the grazing removal on species-rich semi-natural grassland that was grazed by red deer.
- Three years of grazing exclusion caused a net loss of conservation value in the grassland through the loss of species, reduction in density of herb flowering, build-up of litter and increase in grass dominance.
- There was some variation in response across different areas of grassland dependent on biomass accumulation; however, responses to grazing exclusion were in the same direction in all areas.
- Conservation value did not recover in the first six months following grazing resuming. Species loss in particular would make restoration of diversity difficult if grazing was excluded from a large area.
- Even short periods of grazing exclusion on these grasslands would have net conservation losses, potentially long lasting, and are therefore inappropriate as a management tool to protect other communities where species-rich grasslands are present.

2.2 Introduction

In a European context several types of grassland are valued for their plant species assemblages, their associated fauna and their aesthetic value. Annex 1 of the Habitats Directive lists 31 types of natural and semi-natural grassland among its protected communities (Council of the European Communities 1992). These include both natural and semi-natural assemblages that have historically been managed in such a way as to foster biodiversity, usually under low intensity agricultural regimes with a low fertiliser input and grazing by livestock or mowing for hay. Many of these grasslands are dependent on grazing for their existence and characteristic species composition (Ostermann 1998, Halada *et al.* 2011). On productive grasslands, extensive grazing is regarded as an important tool for conservation management (Rosenthal *et al.* 2012). However, grasslands frequently occur in mosaics with other Annex 1 communities, such as heaths, that, whilst also grazing-dependent, require much lower levels of grazing to maintain their conservation value. Managing for the maintenance of conservation value in both communities can be difficult under these circumstances (Holland *et al.* 2010, Halada *et al.* 2011).

Both excessively high, and very low or no grazing of grassland, heathland or rangeland can compromise the productivity of communities used for grazing, agriculture or wildlife, influence their composition, structure, sustainability and above and below-ground ecological interactions with other organisms (Bardgett & Wardle 2003, Mysterud 2006). Extremes of high and low grazing intensity are often referred to as 'overgrazing' and 'under-grazing', respectively. These terms are quantifiable only with reference to specific management goals (Mysterud 2006). On grasslands, loss of, or severe reduction in, grazing tends to lead to loss of smaller, less competitive plant species, a build-up of litter and dominance by a few species of competitive grasses in the shorter term; in the longer-term, invasion of shrubs and trees is common where a seed source exists (Bakker 1998). Compared to more moderate grazing, the negative effects of high grazing pressure include: loss of species unable to tolerate or avoid high grazing pressure and associated trampling; reduction in flowering (which may lead to loss of annuals dependent on being able to set seed every year); and reduction in structural diversity. Increased erosion due to trampling and removal of vegetation is a risk, especially on unstable substrates (Bakker 1998, Sansom 1999). The impacts of grazing vary depending on the timing of grazing (e.g. summer grazing will limit flowering more than winter grazing), and also species of herbivore (e.g. spread of unpalatable tussock grasses is increased under sheep grazing but decreases under cattle grazing as cattle are less selective than sheep (Grant *et al.* 1996b). Lower flowering rates and loss of structural diversity in particular will affect other groups of species dependent on these grasslands, especially invertebrates (Wallis De Vries *et al.* 2002).

In recent decades there have been changes to the use of agricultural land in the EU. This has resulted in abandonment of farming in some areas and intensification in others.

Abandonment has occurred more often in areas of higher farmland biodiversity where agricultural productivity is low, and it has led to declines in diversity (e.g. Bignal & McCracken 1996, McCracken & Huband 2005, Maurer *et al*. 2006), except where increases in numbers of large wild herbivores (e.g. deer) have at least partially replaced grazing pressure on abandoned agricultural areas (e.g. Hope *et al.* 1996, Schutz *et al.* 2003). Recent changes to EU agricultural policy are predicted to lead to further abandonment in areas of high farmland biodiversity, raising conservation concerns (Renwick *et al*. 2013). Some reduction in grazing pressure may benefit communities such as heathland which are frequently overgrazed; exclusion and control of grazing are frequently used tools in the restoration of previously overgrazed moorland (e.g. Hulme *et al.* 2002, ter Braak & Šmilauer 2002). However, if grazing is reduced too far, a net negative impact on conservation value is to be expected, especially on grassland plant diversity (Rural Policy Centre 2008, Renwick *et al.* 2013). Since grassland and heathland frequently co-occur, there is potential conflict in managing for both types of community.

Aims

The aim of this study was to analyse the impact of this potential conflict in grazing requirements on the conservation status of species-rich grassland, by mimicking the impact of large scale herbivore removal. As an exemplar system, it addressed the impacts of grazing exclusion on species-rich, semi-natural grasslands on the Isle of Rum NNR, NW Scotland. This grassland is dependent on grazing to maintain its species richness (Ball 1974) and is present alongside large areas of heath (see Fig 2.1) that has been assessed as overgrazed: >20% of wet and dry heath was classed as overgrazed in a recent survey (Dayton 2008). The exclusion experiment described in this chapter was designed to: (1) quantify the time course of early changes in biomass accumulation, species composition, and diversity in response to grazing exclusion; (2) to assess the speed of recovery from a short period of grazing exclusion and; (3) to relate differences in response to differences in initial species composition and productivity of the grasslands.

2.3 Methods

Field site

The main location for this experiment was in the north of the island in Kilmory Glen (57° 2'54.43"N, 6°21'5.12"W), where there is an area of grassland adjacent to the coast and extending inland for several kilometres along the side of the Kilmory River. A second location was on coastal grassland at Glen Harris (56°58'32.45"N, 6°22'51.39"W), in the south west of the island (Fig 2.1). Grasslands at the mouth of the two glens were used for grazing and subsistence agriculture from Neolithic settlement until 1826, when the original human inhabitants of the island were removed and the island was converted to a sheep walk. For most of the period between 1845 and 1957, the island was heavily grazed by several thousand sheep (up to 8000) and an uncertain number of deer (between 800 and 1800 in the early part of the 20th century) (Pearman *et al.* 2008). In 1957, sheep were removed from the island and it has since been managed as a nature reserve. The remaining large herbivores present are around 900 red deer, approximately 300 feral goats, a herd of approximately 40 Highland cattle and a herd of 20 Highland ponies (Pearman *et al.* 2008, SNH 2010).

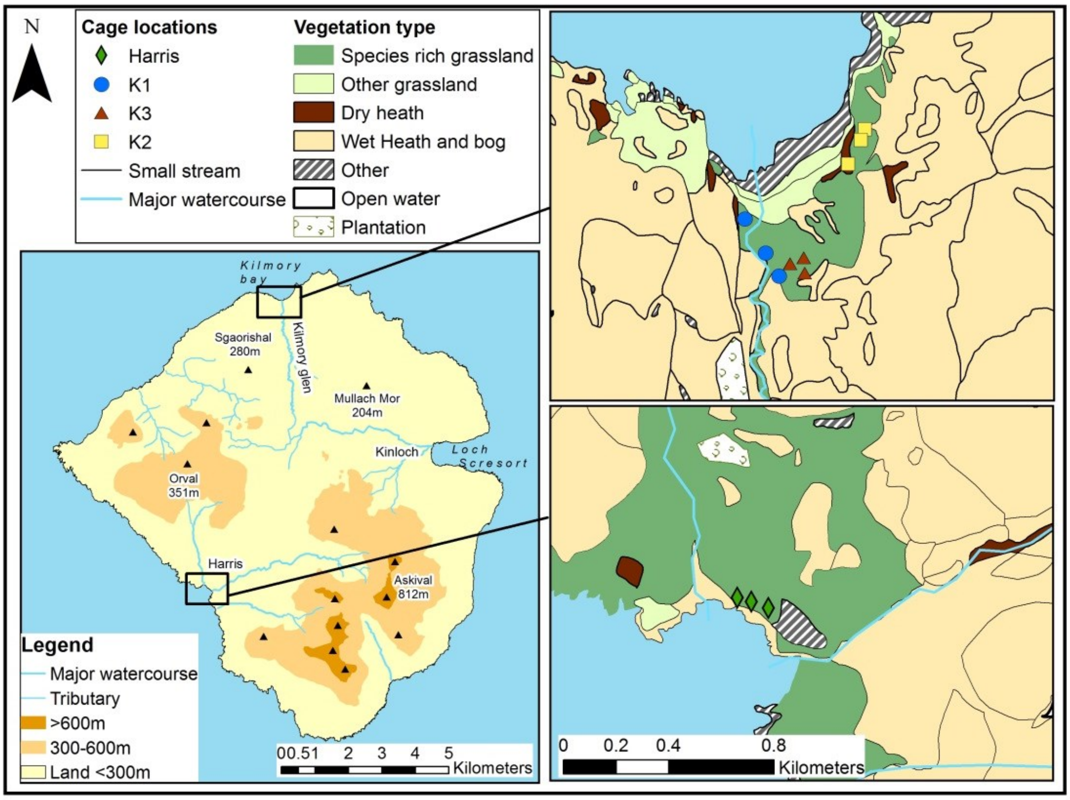

Fig 2.1: Map of location of cages and broad vegetation types in the two parts of the Isle of Rum, Kilmory and Harris, where the study was conducted. Vegetation data from (Bates *et al.* 2002)

Field Methods

Four areas of heavily grazed species-rich grassland were chosen, three areas in Kilmory Glen (referred to hereafter as K1, K2, K3), and one on similar grassland in Glen

Harris (H) (Fig 2.1). The grasslands are classified as 'species-rich *Nardus* grassland', which is listed as a priority habitat type in the EU Habitats Directive (Council of the European Communities 1992). The soils at Kilmory and Harris are brown earth soils, there is basic influence from calcareous, sandy deposits (Ragg & Ball 1964, Pearman *et al.* 2008). Species composition is primarily that of calcareous grassland, although species typical of acid grasslands are present along with (in some places) ericoid shrubs, primarily *Calluna vulgaris*, reflecting the mixed origin of the substrate. The dominant grass species are *Festuca rubra* or *ovina, Agrostis* species and *Poa pratensis*. *Nardus stricta* is present in the grasslands but not dominant.

Red deer (*Cervus elaphus*) are the main herbivores in Kilmory Glen: the annual Deer Commission for Scotland (DCS) counts for the years 2010-2012 found 110-180 deer in the 14 km^2 count area of which Kilmory Glen is a part (6-10 deer km^{-2}) (SNH, pers. comm.). Additionally, a herd of approximately 20 ponies are sometimes present. Harris Glen is grazed by multiple species: 90 feral goats were counted in a 2010 census in the area (SNH, pers. comm.); a herd of approximately 40 cattle and the herd of 20 ponies spend the majority of their time in this area; and 150-200 deer were counted in the DCS deer census area that covers Harris Glen, amounting to 6-8 deer km^{-2} (SNH, pers. comm.; Pearman *et al.* 2008).

In May 2010, within each identified area (K1, K2, K3 and H, see above) three sites were chosen (i.e. a total of 12 sites, nine at Kilmory, three at Harris, see Fig 2.1 for locations). At each site, two cages of dimensions 0.8 m x 0.8 m and 0.6 m high were pegged down (Fig 2.2). Within each cage a 30 cm x 50 cm permanent quadrat was laid out with metal pegs, and a control plot of the same dimensions marked with wooden pegs close to the cages. The percentage cover of each species in each quadrat was estimated by eye. Vascular plants were identified to species level (except in a few cases where early growth stage or grazing made it impossible to determine species) and the cover of bryophytes, litter and bare ground was also recorded. Two 20 cm x 20 cm quadrats were clipped from outside the cages and the total plant biomass collected. A dung count was then carried out in a 2 m x 5 m area adjacent to the site, in which the number of deer pellet groups and individual pellets was recorded along with the number of pony dung piles.

Sites were revisited in November and May in each year until November 2012. Estimates of the cover of each species were repeated in each quadrat. An estimate of one season's productivity was obtained in November 2010 by harvesting total biomass from two 20 cm x 20 cm quadrats inside one of the cages and from two 20 cm x20 cm quadrats outside the same cage (ensuring the quadrats did not overlap with areas sampled in May 2010). The cage from which biomass was harvested was removed so that recovery from short-term exclusion could be monitored. The remaining cage was left *in situ* until November 2012. In November 2012, the final cage was removed and biomass was harvested from inside and outside this cage. The number and species of flower heads in each plot was recorded in May 2011 and 2012.

Following collection, harvested biomass was refrigerated and subsequently frozen, and a subsample (approximately 20% by mass) was later sorted into five fractions (live graminoids, live shrubs, live herbs, moss and dead material). The sorted fractions and the total remaining unsorted material were dried at 80°C for 24 hours and cooled in a desiccator before weighing.

Two cages were lost to attacks by stags during the course of the experiment; their removal was not discovered until the exposed plot had been grazed, so cages could not be replaced. In the first year (2010), one cage from the K3 area was lost so this site had no recovery plot for the first season but retained the second cage for the full period. Another cage was lost from a different site in the K3 area in 2011. Three of the recovery plots were lost in later years as the steel corner pegs could not be relocated.

Fig 2.2: An experimental site as established in May 2010, showing cages, control quadrat and recently clipped quadrats.

Statistical methods

All analyses were carried out in R 2.14.2 (R Core Team 2013). Package nlme was used for linear mixed models (Pinheiro *et al.* 2012), and package vegan was used for multivariate analysis techniques (Oksanen *et al.* 2013).

Analysis of accumulated plant biomass

The total standing crop harvested in November 2010 and November 2012 and the proportion of biomass in each sorted fraction was analysed for differences between caged and control treatments and between the four predetermined Groups of sites in the four grassland areas (K1, K2, K3, H) and for any interaction between Treatment and Group. Linear mixed models were used, with Site as a random effect. The proportion data were transformed using the logit scale before analysis, as follows:

$$\mathrm{Log}_{10}\left((\text{proportion} + 0.001)/\left(1 - (\text{proportion} - 0.001)\right)\right)$$

Botanical species composition

Baseline plant species composition

A principle components analysis (PCA) of the baseline botanical composition was carried out, to test whether the grouping of plots by the four chosen locations corresponded to differences in botanical composition.

Effect of grazing exclusion on species composition

Redundancy analysis (RDA) (Rao 1964), which is analogous to a multivariate regression analysis, was used to explain changes in species composition across all time points using a predetermined set of explanatory variables. Species data (% cover) were log-transformed before analysis (log(x+1)), and the independent variables were Treatment (grazing exclusion, grazing exclusion for one season, control) and Time (as a categorical variable). The interaction between Treatment and Time was tested, with Time and Site included as covariates in the model to account for repeated measures and the pairing of plots within a Site. Principle response curves (PRC) were used to display the trends over the whole time period along the significant axes of the RDA (Van den Brink & Ter Braak 1999). Significance testing was by 499 Monte-Carlo permutations. To account for repeated measures, permutations were restricted so that whole time series were permuted. The second and subsequent axes were tested for significance by adding the sample scores of the preceding axis/axes as a covariate(s) (Van den Brink & Ter Braak 1999).

The analysis was repeated using cover weighted mean trait values in place of species composition. Plant traits from the LEDA and BiolFlora databases were selected (BiolFlor 2004, Kleyer *et al.* 2008). Traits selected were those expected to respond to changes in grazing pressure, primarily those associated with persistence (Weiher *et al*. 1999), and are listed in Table 1. Trait data were standardised so that the mean of each trait was 0 and variance was 1 to account for the differences in units used. Species with no trait data available were ignored for the purpose of these analyses. Plants with no trait data available were mainly individuals that could not be identified to species level. Trait data was available for >95% of total vascular plant cover on all but five occasions (of a total 203 species composition records) and on no occasion was trait data available for less than 85% of plant cover. This small proportion of missing data should have little effect on the analysis (Pakeman & Quested 2007).

Table 2.1: Plant traits from LEDA and BiolFlor database used in multivariate analysis (BiolFlor 2004, Kleyer *et al.* 2008).

Plant traits and abbreviations used	**Values**
Maximum vegetative canopy height,	Numeric (cm)
Leaf dry matter content (LDMC)	Numeric (mg g^{-1})
Specific leaf area (SLA)	Numeric (mm^2 mg^{-1})
Growth form	Rosette, hemi-rosette, erosulate
Start of flowering	Integer corresponding to month
Means of pollination	Wind, insect or self-pollination
Lifespan	Annual, biennial or perennial
Vegetative spread	Rhizomes, stolons or no vegetative spread

As a second approach I tested whether accumulated standing biomass, measured as the difference between the exclusion plot and the freely grazed adjacent control plot, had significant explanatory power for difference in species composition. Accumulated biomass and Time were input as fixed effects to an RDA of the species composition of the first (May 2010) and final (November 2012) time points. The significance of adding a Treatment x Time interaction to the model was also tested.

Other measures of community change

Several other measures of community change were analysed for the effect of grazing exclusion. The response variables chosen were the Shannon diversity index, the number of herb species, the number of graminoid species, % cover of litter and the % cover of bare ground. The effect of grazing exclusion and of group on selected species with high cover values or common to most plots was also tested. The full time-series was analysed using linear mixed effects models fitted with Residual Maximum Likelihood (REML), with the random effect of Site to account for pairing, and the fixed effect(s) were all combinations up to a three-way interaction of Group, Treatment and Time. Time was treated as a categorical variable as seasonal effects were expected. Models were simplified under Maximum Likelihood estimation (ML), by dropping higher order non-significant terms and retesting the significance of remaining terms until a final model containing only significant terms was reached. The final model reported in the results was refitted under REML, p-values reported are those for deletion of terms under ML (Crawley 2007). As a second approach I tested whether the accumulated plant biomass in the control plots explained the above listed community variables in November 2012. The fixed effects in this second model were Time and Accumulated biomass.

The effect of Treatment and Group on total graminoid and herb flower heads per plot and on the number of species flowering per plot was also analysed. Generalised linear mixed models with a Poisson error structure were used as the data were count data. Site was included as a random error term, and the fixed effects were Treatment, Group and Treatment x Group interaction. Treatment had three levels in 2011, as the recovery plots were included, but only the continual exclusion and control plots were analysed in 2012. Since there was no baseline survey of flowering in May 2010 the analyses were conducted using the data from each year separately.

2.4 Results

Baseline species composition

Detrended correspondence analysis (DCA) was performed to assess the suitability of using linear techniques in subsequent analysis. At baseline, the first axis length was 2.1SD, and for all the data, length was 2.4SD, which suggested that linear methods were appropriate (Leps & Smilauer 2003).

Principle component analysis (PCA) of species composition in May 2010 showed that the species compositions mostly clustered according to the groups determined *a priori*. Whilst the Harris and K2 groups are distinct, K1 and K3 had a degree of overlap on the first two axes (Fig. 2.3). A total of 37.0% of the variance was explained by the first two axes.

PCA axis 1 appeared to represent a soil pH gradient: heath species increased from left to right and herbs related to more neutral and base-rich soils increased from right to left. PCA axis 2 was associated with the abundance of a few herb species and also *Carex arenaria*, litter and the grass *Anthoxanthum odoratum*, which were more common at Harris.

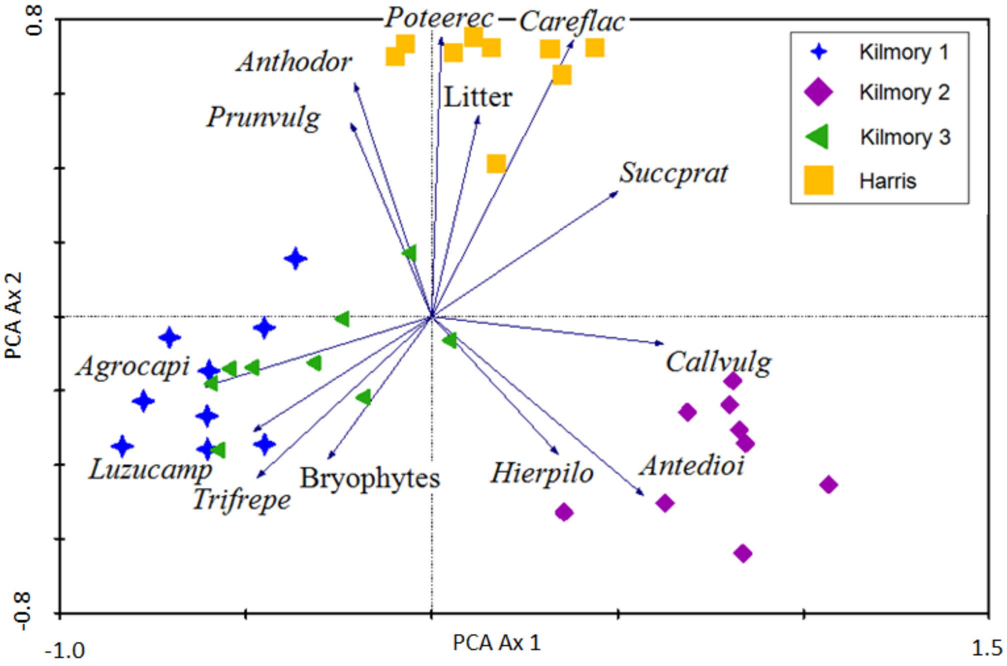

Fig. 2.3: PCA of the baseline species composition of all plots, labelled by the *a priori* determined location groups. For species abbreviations see Appendix II.

Effects of grazing exclusion on biomass accumulation

Total biomass after one growth season (2010)

Grazing exclusion led to an increase in biomass in all four groups of sites. More biomass accumulated in cages in K1 than in the other groups (Treatment x Group interaction p=0.048) (Fig. 2.4).

Biomass fractions after one growth season (2010)

The biomass in each sorted fraction differed slightly between treatments after only one season of grazing exclusion: there was a significantly higher proportion of graminoids (p=0.0012) in the exclusion plots. The only significant interaction between Treatment and Group was for bryophytes (p=0.013): bryophytes accounted for a higher proportion of biomass in the K2 exclusion plots compared to K2 controls, but in other groups bryophytes made up a similar or smaller proportion of the biomass in exclusion plots than control plots (Fig. 2.4; Table 2.2).

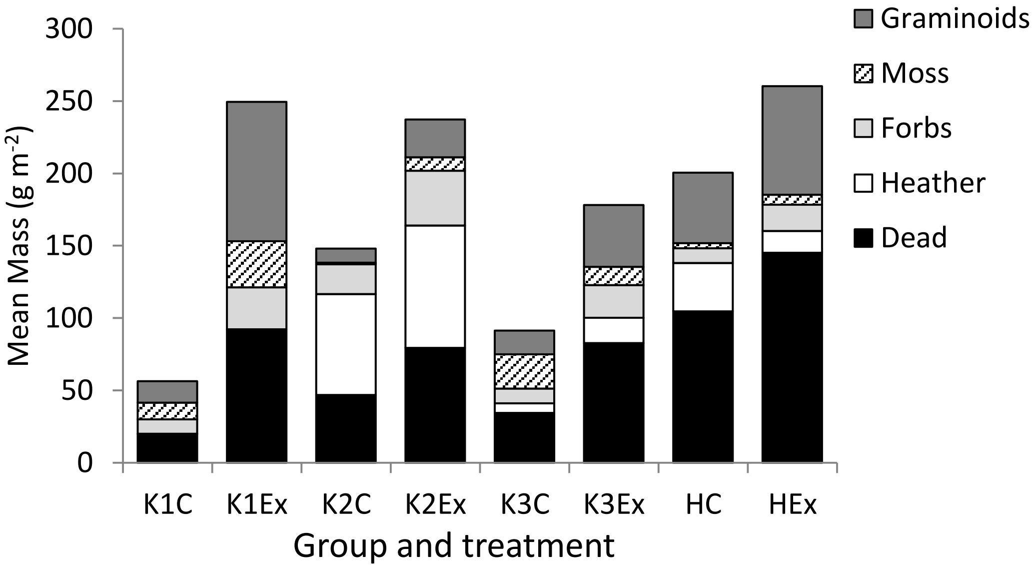

Fig. 2.4: Harvested biomass (g m^{-2}) from cage and control plots Nov 2010, showing sorted fractions. Means for Group and Treatment shown. Ex=Exclusion plots. C=Control plots. K1-3: Groups at Kilmory; H= Harris group.

Total biomass after three growth seasons (2010-2013)

There was a more than four-fold difference in accumulated biomass following exclusion of grazing between the highest biomass (1800 g m^{2}) and lowest biomass (375 g m^{-2}) sites at the end of the third growing season (Nov 2012) (Fig. 2.5). This was visually very obvious (Fig. 2.6). There was a significant interaction between Treatment and Group (p=0.002) on accumulated standing biomass. Standing biomass increased most in the K1 Group and least at Harris (Fig. 2.5).

Biomass fractions after three growth seasons (2010-2013)

After three years' grazing exclusion, the proportion of graminoids and dead material was significantly greater in exclusion plots than controls (p=0.0001; p=0.0017, respectively). There was a significantly lower proportion of moss inside exclusion plots (p=0.0012). The effect of Treatment on the proportion of heather interacted with Group (p=0.017): heather declined as a proportion of total biomass in the Harris group, increased in the K1 group and did not change much in the K2 and K3 groups (Table 2.3; Fig. 2.5). There were no further interactions between Treatment and Group (Table 2.3).

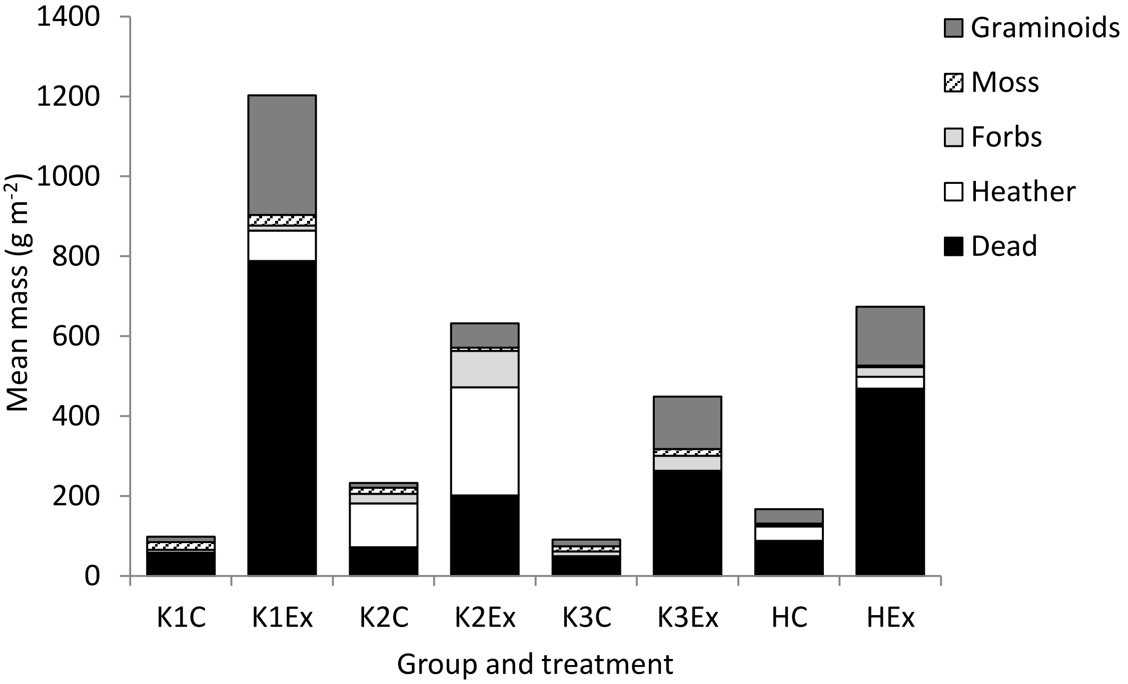

Fig. 2.5: Harvested biomass (g m^{-2}) from cage and control plots Nov 2012, showing sorted fractions. Means for group and treatment shown. Ex=Exclusion plots. C=Control plots. K1-3 = Groups at Kilmory; H = Harris.

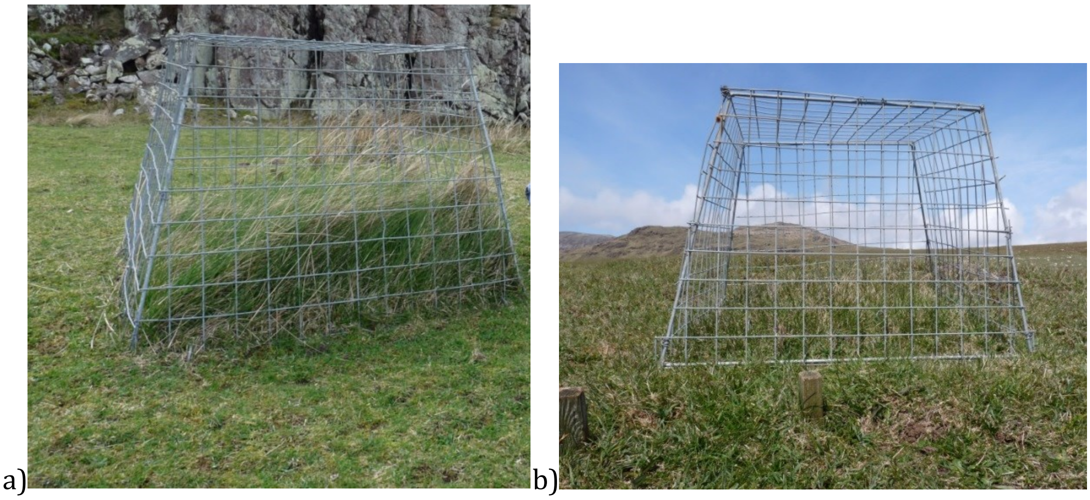

Fig. 2.6: Substantial biomass accumulation at one of the K1 plots, March 2012 (a), and surprisingly little accumulation at Harris, May 2012 (b).

Table 2.2: Effect of Treatment and Group on the contribution of each fraction of biomass to the total in November 2010 after one growth season. Models constructed using logit transformed response. p-value is the value of the deletion of the interaction term from the full model and is shown in bold for significant terms. Where the interaction term is non-significant, p-values are also given for the deletion of main effects from the model without the interaction term. Coefficients are from the model containing only significant ($p<0.05$) or nearly significant ($p<0.10$) terms.

Measurement	Fixed effects	Coefficient	Std Dev	*p-value*
Logit(Dead)	Intercept	0.081	0.0494	
	Treatment			0.520
	Group			**0.0004**
	K1 (vs. H)	-0.288	0.073	
	K2 (vs. H)	-0.407	0.070	
	K3 (vs. H)	-0.225	0.070	
	Treatment x Group			0.298
Logit(Heather)	Intercept	-0.978	0.208	
	Treatment			0.414
	Group			**0.0001**
	K1 (vs. H)	-1.81	0.209	
	K2 (vs. H)	0.693	0.294	
	K3 (vs. H)	-0.748	0.294	
	Treatment x Group			0.920
Logit(Herbs)	Intercept	-1.01	0.102	
	Treatment			0.223
	Group			**0.058**
	K1 (vs. H)	0.346	0.151	
	K2 (vs. H)	0.345	0.145	
	K3 (vs. H)	0.305	0.145	
	Treatment x Group			0.140
Logit (Graminoids)	Intercept	-1.930	0.244	
	Treatment			
	Cage(vs. Control)	0.240	0.345	
	Group			
	K1 (vs. H)	1.22	0.345	
	K2 (vs. H)	0.427	0.345	
	K3 (vs. H)	0.807	0.345	
	Treatment x Group			**0.013**
	Cage:GroupK1	-0.363	0.517	
	Cage:GroupK2	0.595	0.488	
	Cage:GroupK3	-0.903	0.488	

Table 2.2: cont.

Measurement	Fixed effects	Coefficient	Std Dev	*p-value*
Logit (Bryophytes)	Intercept	-0.353	0.081	
	Treatment			**0.0012**
	Cage (vs. Control)	0.181	0.064	
	Group			**0.0001**
	K1 (vs. H)	0.102	0.109	
	K2 (vs. H)	-0.567	0.106	
	K3 (vs. H)	-0.191	0.106	
	Treatment x Group			0.270

Table 2.3: Effect of Treatment and Group on the contribution of each fraction of biomass to the total in November 2012 after three growth seasons. p-value is the value of the deletion of the interaction term from the full model. Where the interaction term is non-significant p-values are also given for the deletion of main effects from the model without the interaction term. Coefficients are from models containing only significant (p=<0.05) or nearly significant (<0.10) terms.

Measurement	**Fixed effects**	**Coefficient**	**Std Dev**	***p-value***
Logit(Dead)	Intercept	0.285	0.060	
	Treatment			**0.0017**
	Cage	0.164	0.052	
	Group			**0.0001**
	K1 (vs. H)	-0.014	0.077	
	K2 (vs. H)	-0.514	0.077	
	K3 (vs. H)	-0.154	0.086	
	Treatment x Group			0.112
Logit(Heather)	Intercept	-1.13	0.290	
	Treatment			
	Cage	-0.736	0.360	
	Group			
	K1 (vs. H)	-0.303	0.410	
	K2 (vs. H)	0.873	0.410	
	K3 (vs. H)	-1.20	0.458	
	Treatment x Group			**0.017**
	Cage:GroupK1			
	Cage:GroupK2	1.567	0.509	
	Cage:GroupK3	0.682	0.509	
		0.591	0.569	
Logit(Herbs)	Intercept	-1.11	0.108	
	Treatment			0.765
	Group			**0.0042**
	K1 (vs. H)	-0.163	0.152	
	K2 (vs. H)	0.377	0.152	
	K3 (vs. H)	0.477	0.190	
	Treatment x Group			0.109
Logit	Intercept	-0.129	0.078	
(Graminoids)	**Treatment**			**0.0001**
	Cage	0.269	0.050	
	Group			**0.0002**
	K1 (vs. H)	-0.063	0.105	
	K2 (vs. H)	-0.669	0.105	
	K3 (vs. H)	-0.094	0.118	
	Treatment x Group			0.475

Table 2.3: cont.

Measurement	**Fixed effects**	**Coefficient**	**Std Dev**	***p-value***
Logit (Bryophytes)	Intercept	-2.23	0.243	
	Treatment			**0.001**
	Cage	-0.550	0.163	
	Group			**0.011**
	K1 (vs. H)	1.04	0.323	
	K2 (vs. H)	0.225	0.323	
	K3 (vs. H)	1.15	0.361	
	Treatment x Group			0.135

Effects of grazing exclusion on species composition

The first and second PRC axes described significant variation in species composition (p=0.001; p=0.005), the third axis was non-significant (p=0.505). Overall, the Treatment x Time interaction explained 6.2% of the variance.

On the first axis, the species that increased over time in the exclusion plots were several grass species and litter. Species that declined in exclusion plots included bryophytes, the low growing herbs *Thymus polytrichus* and *Plantago maritima. Carex pulicaris* and the less competitive grass species *Poa pratensis* also decreased, as did bare ground. Changes on the first axis were most rapid in the first season and gradually slowed over time (Fig. 2.7). The second axis appears to represent seasonal modification of the strength of the effect of exclusion on the species that were correlated with the first axis: plots do not change much on the second axis in the first season, and from May 2011 there is a seasonally varying effect (Fig. 2.8). In the treatment where grazing was excluded for only one season, species composition recovers almost to the start point by May 2011 on both axes, and by November 2011 appears to have completely recovered.

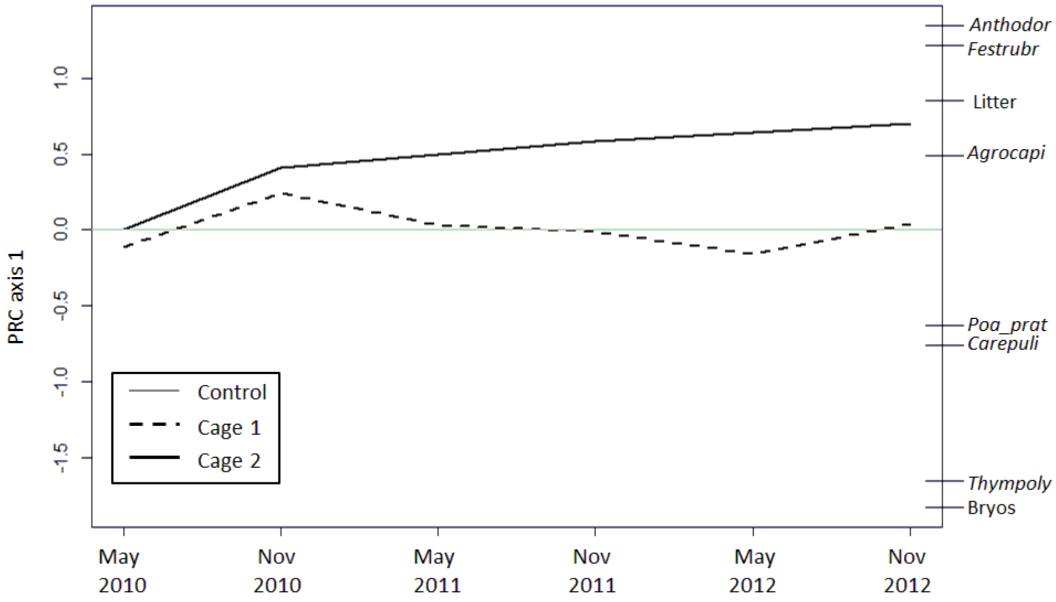

Fig. 2.7: PRC axis 1 showing the effect of Treatment x Time on species composition of the exclusion and recovery plots as compared to control plot composition. Cage 1 yr is the set of recovery plots, Cage 3 yr is the plots that were caged until November 2012. Species shown are the eight with strongest association with the axis. Bryos = Bryophytes; *Anthodor = Anthoxanthum odoratum; Agrocapi = Agrostis capillaris*; *Carepuli = Carex pulicaris; Festrubr = Festuca rubra; Planmari = Plantago maritima*, *Poa_prat = Poa pratensis*, *Thympoly =Thymus polytrichus.*

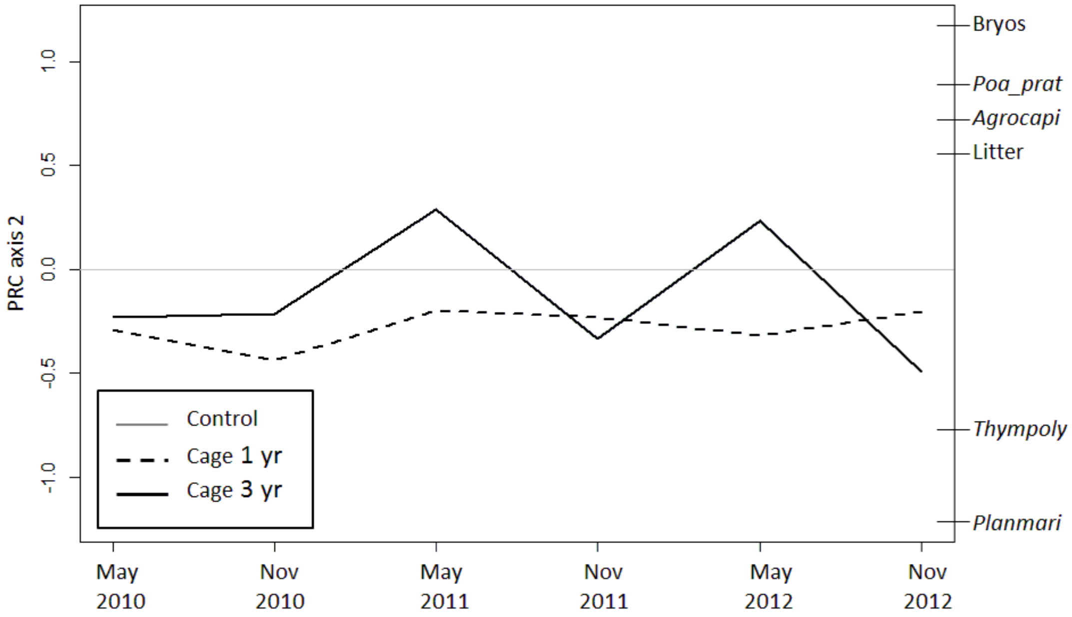

Fig. 2.8: PRC axis 2 showing the effect of Treatment x Time on species composition of the exclusion and recovery plots as compared to control plot composition. Cage 1 yr is the set of recovery plots, Cage 3 yr is the plots that were caged until November 2012. *Agrocapi* = *Agrostis capillaris*; *Planmari* = *Plantago maritima*; *Poa_prat* =*Poa pratensis; Thympoly =Thymus polytrichus.*

Effect of grazing exclusion on the traits of the plant community

The Treatment x Time interaction explained 6.8% of the variance in traits. The first axis of the PRC was significant (p=0.01) explaining 8.4% variance (including the effect of covariates). Subsequent axes were not significant. The exclusion plots increased in score on the first axis of the PRC in the first season. This corresponded to an increase in: canopy height, wind pollination, beginning of flowering, hemi-rosette growth forms and LDMC; and a decline in rosette growth forms and other forms of pollination (Fig. 2.9). Following cage removal in November 2010, the one season's exclusion plots returned to their start point gradually, while the three year exclusion plots continued to diverge from the controls over time.

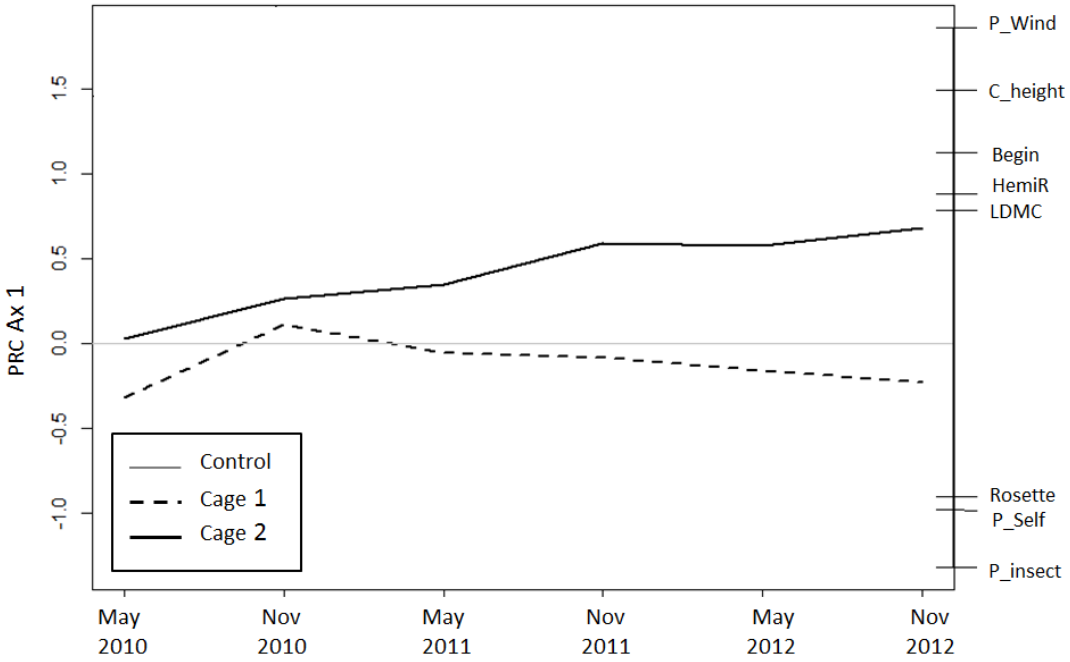

Fig. 2.9: PRC axis 1 of traits. Cage 1 is the set of plots whose cages were removed in November 2010; Cage 2 is the plots that were caged until November 2012. Traits are highest scoring on the axis. P_Wind, P_Self, P_insect = Wind, self and insect pollinated; C_height = canopy height, Begin = beginning of flowering, Rossette= rosette growth form, HemiR = hemi-rosette form, LDMC = Leaf Dry Matter Content.

Accumulated biomass and species composition

The first axis of the RDA accounted for 13.2% of the species variance, which was significant (p=0.005). 4.8% was attributable to accumulated biomass, the rest to covariates. The addition of a Treatment x Time interaction to the model increased total explanatory power to 18.2% (7.2% attributable to fixed effects) and first axis explanatory power to 14.3% (including the effect of the covariates Site and Time). However the first RDA axis was non-significant with the interaction included (p=0.088). Species responding to accumulated biomass increase show a similar pattern to those responding to treatment over the whole period (compare Fig. 2.7 and Fig. 2.10). Grasses increased with increasing biomass but small herbs decreased.

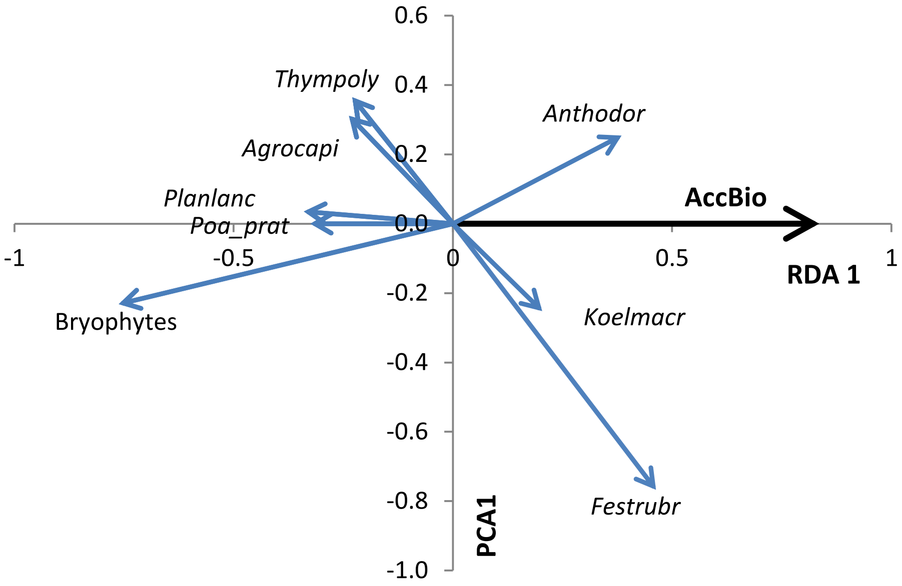

Fig. 2.10: RDA plot of accumulated biomass in November 2012, showing species with highest scores on the constrained axis. AccBio arrow indicates the direction of the effect of increasing accumulated biomass. Species are: *Agrocapi* = *Agrostis capillaris; Anthodor = Anthoxanthum odoratum; Festrubr =Festuca rubra; Koelmacr = Koeleria macrantha; Poa_prat = Poa pratensis; Planlanc = Plantago lanceolata; Thympoly =Thymus polytrichus*

Accumulated biomass and changes to the traits of the plant community

Accumulated biomass accounted for 5.54% of the variance in trait data and has significant explanatory power (p=0.01, RDA axis 1 =11.8%, compared to PCA axis 1 = 31.5%). The addition of a Treatment x Time interaction to the analysis increased constrained variance to 8.25% but this was non-significant (p=0.470). Again traits correlated with accumulated biomass were similar to those correlated with the exclusion treatment over the whole time period (Fig. 2.9; Fig. 2.11). Trait changes indicate an increase in taller growth forms in high biomass plots (increase in canopy height and hemi-rosette species and a reduction in rosette growth forms), and an increase in wind pollinated species (mainly graminoids), a decrease in other forms of pollination, as well as an increase in LDMC and a decrease in leaf size.

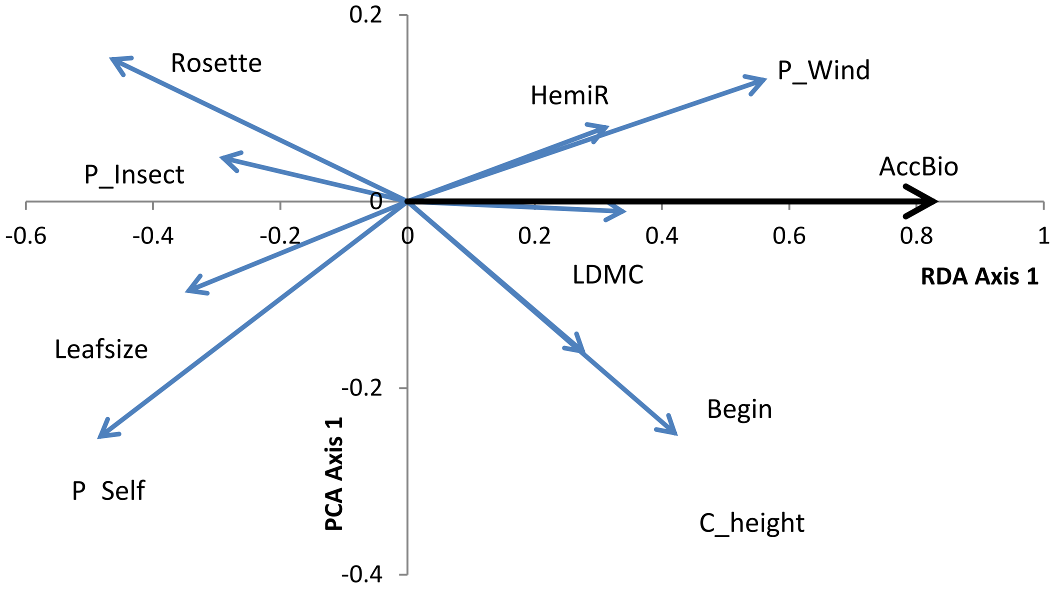

Fig. 2.11: Traits and accumulated biomass RDA showing highest scoring traits on the RDA axis. LDMC = leaf dry matter content; P_Wind, P_Self, P_insect = Wind, self and insect pollinated; C_height = canopy height, Begin = beginning of flowering, HemiR = hemi-rosette form. AccBio = accumulated biomass, Leafsize = Leaf size

2.5 Changes in vegetation species diversity, structure and flowering, following exclusion of grazing

Effect of grazing exclusion

Exclusion of grazing caused decline in herb species number and Shannon diversity index from the end of the second year of exclusion (Fig. 2.12a, e). There was no effect on graminoid species number (Fig. 2.12f). Cover of bare ground decreased, and litter cover increased (see Fig. 2.12b, d). There were no three way interactions with Group. There was one significant two-way interaction between Treatment and Group: cover of litter did not increase as much in K2 Group exclusion plots as in other areas (see Fig. 2.12c).

There was no effect of treatment on the number of species which flowered in either 2011 or 2012 (Fig. 2.13a, c), although there were some differences between groups (Fig. 2.13b, d). The number of herb flower-heads was lower in exclusion plots, significantly in 2012 (Fig. 2.13e). The number of graminoid flower-heads was higher inside the exclusion plots than in controls, in both years (Fig. 2.13g). There were differences in herb flower-head number between groups in 2012 (Fig. 2.13f) and differences in graminoid flower-head number between groups in both years (Fig. 2.13h). It was not possible to test the interaction of Group and Treatment in some cases, due to failure in convergence of the models. Where it was possible to test the interaction, it was non-significant.

Effect of accumulated biomass

Biomass accumulation was negatively correlated with diversity and herb species number and positively correlated with litter and graminoid cover in November 2012 (Table 2.4).

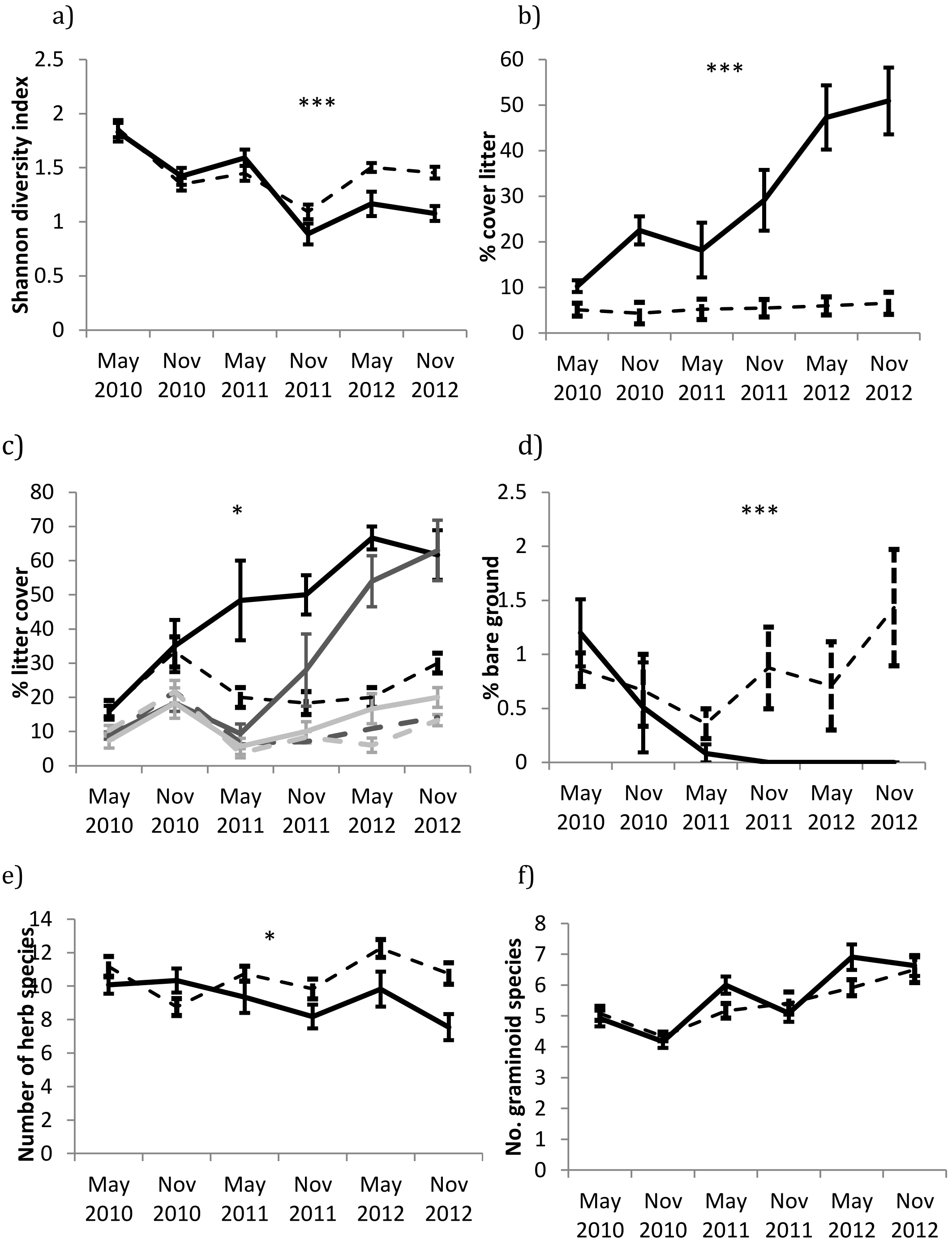

Fig. 2.12: Changes in community measures over time in exclusion (solid line) and control (dashed line) plots. Error bars = 1 S.E. p-values of Treatment x Time interaction given in brackets a) Shannon diversity index, (p<0.0001) b) Percentage cover of litter treatment x time p<0.0001 c) Litter showing interaction between Treatment and Group (p=0.029). Black =Harris; dark grey = K1&3; light grey = K2 d) percentage cover of bare ground (p=0.044); e) mean herb species number (p<0.0001) and f) mean graminoid species number (p=0.048).

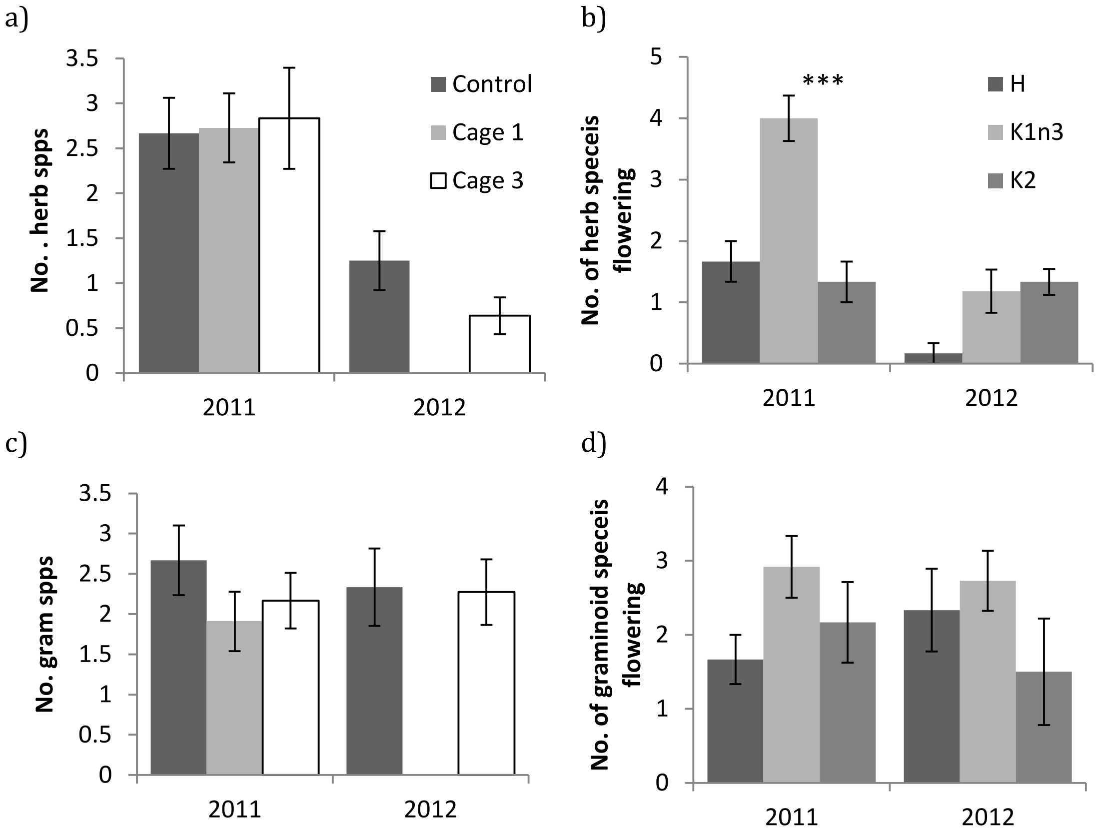

Fig. 2.13: Differences in flowering by Treatment (left hand column) and Group (right hand column). Stars indicate significant differences between Treatments and Groups in particular years.*=p<0.05, **=p<0.01; ***= p<0.001. There were no significant interactions between Treatment and Group in 2011 (models containing interactions did not converge for 2012 data). The data from both the exclusion for one season (Cage 1yr) and exclusions for three seasons (Cage 3yr) Treatments were included in the analysis of the 2011 data. Only the Control and continually caged plots were included in the 2012 data analysis.

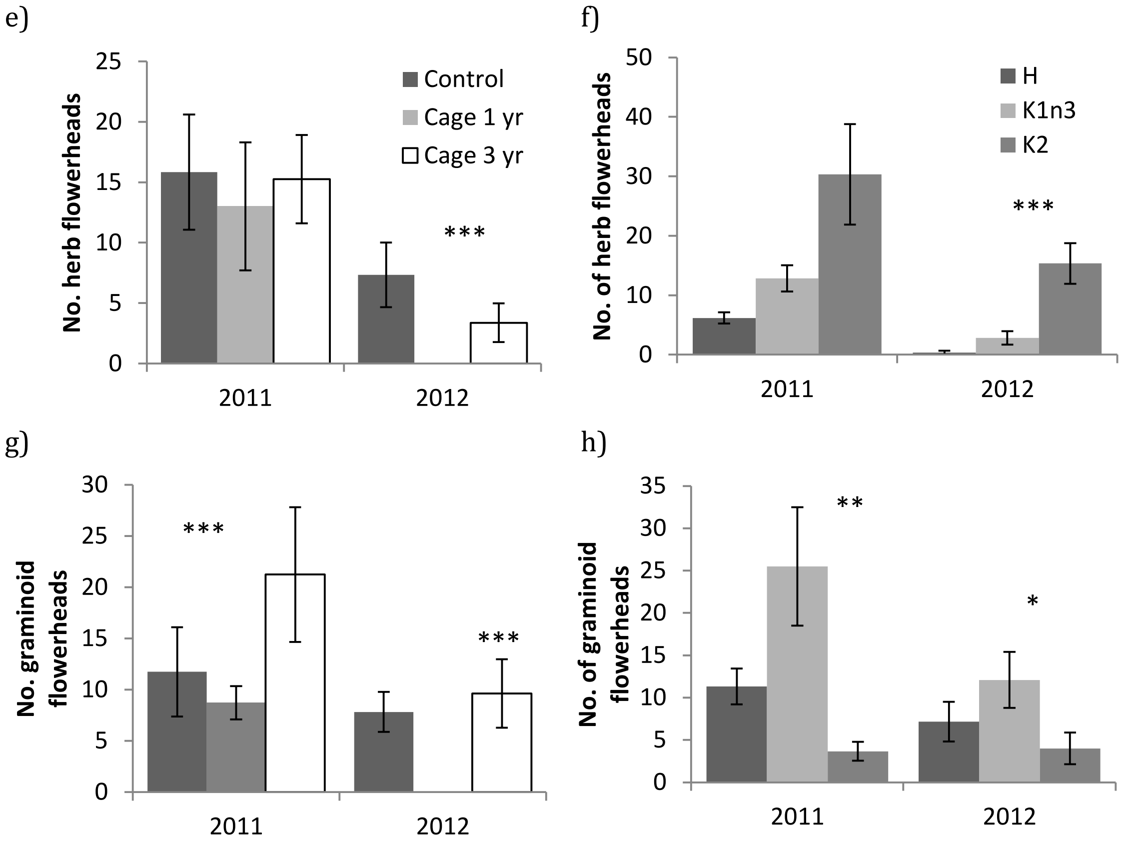

Fig 2.13 cont. Differences in flowering by Treatment (left hand column) and Group (right hand column). Stars indicate significant differences between Treatments and Groups in particular years.*=p<0.05, **=p<0.01; ***= p<0.001. There were no significant interactions between Treatment and Group in 2011 (models containing interactions did not converge for 2012 data). The data from both the exclusion for one season (Cage 1yr) and exclusions for three seasons (Cage 3yr) treatments were included in the analysis of the 2011 data. Only the Control and continually caged plots were included in the 2012 data analysis.

Table 2.4: Diversity and structural measures compared with accumulated biomass after three seasons' grazing exclusion. AccBio= accumulated biomass in exclusion plots minus that harvested from the paired control plot in November 2012.

Measurement	Fixed effects	Coefficient	Std Dev	p-value
Shannon diversity index	Intercept	1.87	0.518	
	Time Nov2012	-0.647	0.083	
	AccBio	$-4.52e^{-4}$	$1.24e^{-4}$	**0.0005**
Log(Bare ground+.1)	Intercept	-0.187	0.241	
	Time Nov2012	-0.581	0.385	
	AccBio	$-1.77e^{-3}$	$5.77e^{-4}$	**0.003**
Log(Litter)	Intercept	2.290	0.141	
	Time Nov2012	0.536	0.117	
	AccBio	$1.49e^{-3}$	$1.61e^{-4}$	**0.0001**
No. of herb species	Intercept	10.7	0.516	
	Time Nov2012	-0.288	0.727	
	AccBio	-0.004	0.001	**0.0006**
No. of graminoid species	Intercept	4.95	0.233	
	Time Nov2012	1.41	0.333	
	AccBio	$4.42e^{-4}$	$5.05e^{-5}$	0.368

2.6 Discussion

Effect of exclusion of grazing on species-rich grassland

This study addressed the extreme case of short-term removal of grazing from species-rich grassland to benefit adjacent communities with different grazing requirements. Brief periods of grazing exclusion on species-rich grassland can benefit conservation goals by increasing vegetative spread and flowering of herbs species (Bakker 1998, Ford *et al.* 2012), but the period of benefit appears not to exist on this grassland. Three years of grazing exclusion caused a net loss of conservation value in the grassland though loss of characteristic species, reduction in density of herb flowering, build-up of litter and increase in grass dominance. Overall the grassland showed a transition to a more species poor, grass-dominated sward.

Removing grazing for three growing seasons produced a significant shift in species composition, decrease in diversity, particularly of herb species, and an increase in litter and graminoids. This response is typical of productive swards where light is the limiting resource (Huisman & Olff 1998, Olff & Ritchie 1998). The grasses that became dominant were mainly *Festuca* and *Agrostis* species, which were some of the most abundant grasses present at the start. Taller, tussock forming grasses which can dominate following loss of grazing such as *Molinia* and *Deschampsia* are not present on these grasslands. *Nardus* was present in some plots but its cover was not increased by grazing exclusion in this experiment. The herb species declining in exclusion plots were low-growing species such as *Thymus polytrichus* and *Plantago* spp. Changes in the proportion of different growth forms present (increase in canopy height, decrease in rosette architecture) were consistent with global trends found when comparing grazed and ungrazed grasslands (Díaz *et al.* 2007). The shift to wind pollinated species and later flowering was mainly due to the increase in graminoids and the decline in herb species. LDMC is positively correlated with slower growing strategies and is generally found to increase in response to decreased grazing or other disturbance. Increasing LDMC indicates a shift towards lower nutrient concentration in the leaf, and less productive species (Grime 2001, Garnier *et al.* 2007) and this would likely result in slower decomposition of the litter layer and reduced rates of nutrient turnover (Fortunel *et al.* 2009).

The main effect of exclusion of grazing on flowering was to increase the number of graminoid flower-heads in exclusion plots. This is as expected; more graminoids are able to reach the reproductive stage following release from grazing. There was also a reduction in herb flowering in 2012, indicating that the effect of light competition outweighed any benefit from the release from grazing. Other studies have found a brief period when herb flowering is increased following grazing exclusion and before increased light competition leads to a reduction in low-growing species (Bakker *et al.* 1997). I did not find this effect on flowering, although as flowering was not measured in the first growing season any differences between treatments in the first season's flowering would have gone unnoticed. Negative effects are not apparent in the first season of exclusion, there is no significant effect on cover of litter, herb species number or Shannon diversity index over the first growing season (see 0 for analysis including all exclusion plots in the first year), although the proportion biomass made up by graminoids has increased. However, nor is there any significant increase in herb species, herbs as proportion of biomass, or diversity. This indicates that the window of potential positive effects of removing grazing from heavily grazed, productive grassland is very short; in this study it was undetectable, if it occurred at all.

However, a short period of exclusion is not equivalent to lighter grazing over a longer period; changes to herb cover and diversity under lighter grazing would also depend on herbivore selectivity under a changed grazing regime.

Effect of biomass accumulation on change following grazing exclusion

The shift in species composition and associated composition of traits, and species number and diversity changes were all correlated with biomass accumulation: there was a greater shift in species composition and a greater reduction in diversity where biomass accumulation was greatest. It is a general finding that grassland community response to changed grazing regime depends on the productivity or standing biomass (Olff & Ritchie 1998, Cingolani *et al.* 2005, Schultz *et al.* 2011, Lezama *et al.* 2014). On high produtivity grasslands, light is limiting and selective grazing on the more competitve species can increase diversity by allowing smaller species to survive, only at very high grazing levels does diversity decrease again as more species become unable to avoid or tolerate grazing. Highest diversity is found at some intermedaite level of grazing following the predictions of the intermediate disturbance hypothesis (Hobbs & Huenneke 1992); by contrast, diversity on low productivity grasslands (not light limited) may be little changed by grazing or even reduced (Olff & Ritchie 1998, Huisman *et al.* 1999). The productivity at which selective grazing causes a decrease rather than an increase in diversity, was predicted by simple theoretical model to be around 300 g m^{-2} annual NPP (Huisman *et al.* 1999) and one study of the effect of grazing exclusion on grasslands across several continents and a range of productivities found that the actual productivity level at which grazing tends to increase rather than decrease diversity is close to this predicted value (~250 g m^{-2}) (Bakker *et al.* 2006). However, there was much variation around this value in that study. Additionally, the expected effect of grazing should depend on the length of coevolution between plants and herbivores in the region; the longer the coevolution, the more plant species in the region would be adapted to grazing and the more likely herbivory is to cause an increase rather than a decrease in diversity compared to ungrazed areas (Cingolani *et al.* 2005, Schultz *et al.* 2011).

Our grasslands showed low productivity and total biomass in the first season, clippings from the most productive group (K1) had a mean total biomass of only 249 g m^{-2}. However, following three seasons' grazing exclusion, total live biomass was higher in exclusion plots than in the first season; additionally, dead biomass had accumulated. Dead biomass will also contribute to the exclusion of smaller species by smothering the ground layer increasing the effects of light competition from taller species. The resulting total biomass (Group means between 499 and 1203 gm^{-2}) is well into the range where reductions in diversity are expected following removal of grazing (Huisman & Olff 1998).

Recovery from grazing exclusion

The effects of three seasons' grazing exclusion on the community composition, flowering and diversity of the community did not recover in the first six months following grazing being allowed to resume. Species losses would make complete recovery to pre-exclusion diversity a long process. Attempts to restore plant species richness by reintroducing grazing can have poor results, if there is no local seed source or seed bank from which the desired species can re-establish (e.g. Bakker 1987, Bakker & Berendse 1999, Willems 2001, Matejkova *et al.* 2003, Piqueray & Mahy 2010).

Conclusions

Exclusion of grazing from species-rich grasslands, either to protect the grasslands from potential overgrazing or other habitats in the area which are more sensitive to grazing, is likely to lead to rapid loss of conservation value on species-rich grassland. In grasslands of a similar productivity range as those in this study, even short-term exclusion of grazing for a few years to benefit other communities would put the grassland at risk. This suggests that periods of exclusion of grazers would have net conservation losses for grassland, potentially long lasting, and are therefore inappropriate as a management tool where species-rich grasslands are present. Changes in plant diversity and sward structure that follow grazing exclusion will impact on invertebrate communities with further consequences for higher tropic levels and nutrient cycling (Borcard *et al.* 1992, Tscharntke & Greiler 1995). Some of these impacts may be beneficial to conservation, for example, grazing exclusion can increase the abundance and diversity of some groups of grassland invertebrates, which increases food resources for birds of conservation concern (e.g. Woodcock *et al.* 2005, Legendre *et al.* 2011).

A very short period of exclusion (one growing season) produced changes that were rapidly reversible, and less productive grasslands would be expected to have a longer period of resilience to under-grazing. The risk to the grassland flora from loss of or severe reduction in grazing will also be less in more exposed areas, as they will not see such rapid accumulation of litter that smothers plants beneath it. However, it is not possible to wholly predict the response of grassland based on simple measurements of annual productivity: although in general the effect of herbivory on grassland is dependent on productivity, the critical level at which grazing or other disturbance becomes necessary to maintain diversity does not appear to be universal. Secondly, as we have demonstrated, measurement of the annual NPP over a single year can seriously underestimated the potential for further biomass accumulation, due to accumulation of dead material and increases in NPP following changes in species composition.

Voles are not present on Rum, but where voles are present exclusion of large herbivores over a large area can cause an increase in their numbers (Hill *et al.* 1992, Hope *et al.* 1996), which can have an effect on subsequent vegetation change. Although diversity still tends to decline, high numbers of voles have been found to prevent total dominance of graminoids in some previous studies (Hill *et al.* 1992). However, in the absence of some disturbing factor maintaining an open sward, removing grazing from species-rich grassland is likely to cause a rapid conversion, within a few years, to a taller and more species-poor sward, from which it would be hard to recover the original composition.

When considering a mosaic of habitats where some are negatively and some positively impacted by grazing (as is the case on the Isle of Rum NNR), protecting the negatively impacted community may come at a severe cost to the other community. Careful consideration of the possible conservation gains and losses for both plant communities and for the associated fauna will be necessary before a course of action can be decided upon. In the case of moorland restoration, positive changes in species composition of moorland are often seen within 3-5 years of grazing exclusion (e.g. Littlewood *et al.* 2006). However this time period is not necessarily sufficient for complete restoration and even this period of exclusion could be severely detrimental to grassland. Extensive grazing has also been successfully used to restore moorland communities (Hulme *et al.* 2002, Pakeman *et al.* 2003, Mitchell *et al.* 2008) and this is would be a preferable option if grasslands of conservation importance were also present.

Chapter 3: Response of species-rich grassland to a reduction in grazing, and the consequences for conservation management of this community

3.1 Summary

- Grazing is an important influence on the structure and diversity of grassland communities. One of the main tools in vegetation community management with large free-ranging (wild) herbivores is reducing the level of grazing.
- However because a reduction in grazing intensity can usually only be brought about by management of the animal populations themselves, there is a shortage of studies on the effects of partial grazing reduction by wild and free ranging herbivore species. In contrast, predictions of the effects of reduced grazing are often extrapolated from total grazing exclusion studies. One reason for this is the cost, especially of a long-term experiment.
- I experimentally imposed a partial reduction in grazing intensity (mainly by red deer) by using a cheap and novel semi-permeable fencing technique. I assessed the subsequent vegetation responses of intensively grazed grassland communities to this reduction in grazing.
- The method was successful in reducing grazing and is a viable alternative to more conventional methods in long-term studies which require significant funding for maintaining large areas of differing herbivore densities.
- Sward height increased in all reduced grazing plots compared to controls. Due to the short time period of the study, I found no change in overall species composition.
- There were some changes to the cover of common plant species, and cover of litter, bare ground and board functional groups, these were related to an interaction between Treatment and Starting height, indicating that initial conditions had a strong influence on the response to reduction of grazing.
- There were some changes in flowering, which could potentially influence future community change, although the reduced cover of bare ground in fenced plots

indicated reduced grazing would result in a reduction in the total effect of flowering on species composition.

- In Chapter 3b, the results of partial reduction in grazing are assessed in terms of their consequences for the conservation value of the grassland. Results are compared to conservation targets that are used to guide management at the site.
- The differences in starting condition meant that the shortest plots benefitted from reduced grazing in terms of fit to some of the SCM targets, notably height targets. The taller plots did not benefit or moved further from meeting targets.
- Reducing grazing over the whole grassland would benefit some areas but be to the detriment of others. The balance of the costs and benefits for the grassland and other communities present (heaths) would have to be considered before changing management.

Chapter 3a: Response of species-rich grassland to a reduction in grazing

3.2 Introduction

Grazing is an important, often dominant influence on the structure and diversity of grasslands (Milchunas & Lauenroth 1993). Although with domesticated herbivores experimental variation of grazing pressure can be achieved through manipulation of herbivore numbers within experimental plots, this is rarely a viable option with wild herbivores, most studies of which use total exclusion techniques and thereby compare vegetation responses of a grazed situation with complete removal of herbivores e.g. (Milchunas & Lauenroth 1993, Díaz *et al*. 2007). Information from these studies is of limited use in predicting the effects of reduced herbivory (Marriott *et al*. 2004), the effects of zero grazing levels are well known from these, but the grazing level outside of the grazing exclusion area is often not well characterised in such studies. Changes to grazing regime, without total exclusion of herbivores, is one of the main tools in vegetation community management by large herbivores, which can be effected by reduction in livestock or management of wild herbivores by culling (Gordon *et al*. 2004, Rosenthal *et al*. 2012). In this chapter I apply a novel technique of partial reduction in grazing via semi-permeable fencing to in order to assess the vegetation responses of intensively grazed grassland communities, grazed mainly by red deer, to reductions in the effective grazing intensity.

Grasslands and grazing

Grasslands and other open habitats are usually dependent on some level of disturbance to maintain their existence (except in situation where abiotic factors prevent tree growth e.g. above alpine treelines), important types of disturbance that maintain grasslands globally are grazing and burning (Belsky 1992, Hejcman *et al*. 2013). Mechanical cutting under cultivation is also important in places (Wallis De Vries 1998, Hejcman *et al*. 2013). Changes to grazing regime in grassland areas can lead to large change all aspects of grassland ecology including: plant and animal species composition, sward structure, nutrient turnover (Hobbs 1996, Bardgett & Wardle 2003). Light to moderate grazing on grasslands can prevent shrub encroachment, increase diversity by decreasing light competition between plants and, on a sward where the majority of plants are palatable, often increases structural heterogeneity (Hobbs & Huenneke 1992, Huisman *et al*. 1999). High grazing intensities can lead to lower diversity, local extinction of species, and in extreme cases soil erosion, a decline in productivity in the long term (Wilson & Macleod 1991, Evans 1997).

Exclusion & reduction of grazing studies

The effects of herbivory are dependent on many factors including, plant community productivity, species of grazer present, season of grazing, and regional plant species pool, amongst others. There have been many studies on grazing exclusion from grasslands worldwide, and several reviews on the subject, enough to make establish some general rules about expected responses to exclusion of large herbivores from previously grazed areas and the nature of the dependence on productivity and other attributes of the grassland (Milchunas & Lauenroth 1993, Bakker *et al*. 2006, Díaz *et al*. 2007). Fewer studies have looked at the impacts of reduced grazing rather than exclusion, and most of these have been in small, enclosed areas, often under agricultural production. But see Marriott *et al*. (2004) for a review of some studies of grazing reduction on semi-natural grasslands, (see also Austrheim *et al*. 2008). Studies in an agricultural context, focussed on animal production, and often on sown swards have little relevance to addressing the effects of grazing in relation to the conservation of semi-natural grassland, as in an agricultural setting nutrient levels are unusually high and species composition of low diversity.

The results of exclusion are often extrapolated to predict plant (community) responses to reduced grazing. However, exclusion experiments are of limited use in predicting the response of a plant community to grazing reduction where responses are non-linear. Although some species have been found to respond to a grazing gradient in a linear fashion, a substantial proportion do not (Pakeman 2004, Pakeman & Marriott 2010). Grassland plant diversity response is often non-linear, peaking at intermediate grazing levels (Hobbs & Huenneke 1992, Cingolani *et al.* 2005). Threshold effects are also possible, in which heavy grazing can cause a step change from one type of ecosystem to another in areas where alternate stable states are possible (Friedel 1991). Additional factors such as the species of grazer and timing of grazing are important, and cannot be extrapolated from exclusion experiments. For example, timing of grazing can affect the impact on a dominant or invasive species (Grant *et al.* 1996a, Grant *et al.* 1996c, Rinella & Hileman 2009). Different species of herbivores exhibit different selective preferences, which can result in different consequences for plant species composition and the spatial pattern of grazing (Prache *et al*. 1998, Nolte *et al*. 2014)

One reason that there are fewer reduced grazing studies compared to exclusion studies, especially fewer long-term studies, is the cost of maintaining different densities of animals for many years (Marriott *et al*. 2004). Here I explore a novel method of grazing reduction that could be used with either wild or domestic stock in an extensive grazing situation that should be less costly than conventional methods of maintaining different grazing intensities, i.e. maintaining large fenced areas of different densities of livestock or establishing and maintaining different densities of wild herbivores by continual culling.

Aims

The aim of this experiment was determine the short term effects of reducing but not excluding grazing from a semi-natural, species-rich grassland of high conservation value. We used a cheap and novel method to reduce grazing pressure that is suitable for use with wild herbivores, using low fencing that allowed deer to enter but made access more difficult, leading to reduction but not total removal of grazing. The success of the method and the benefits and drawbacks in comparison to more conventional methods are discussed.

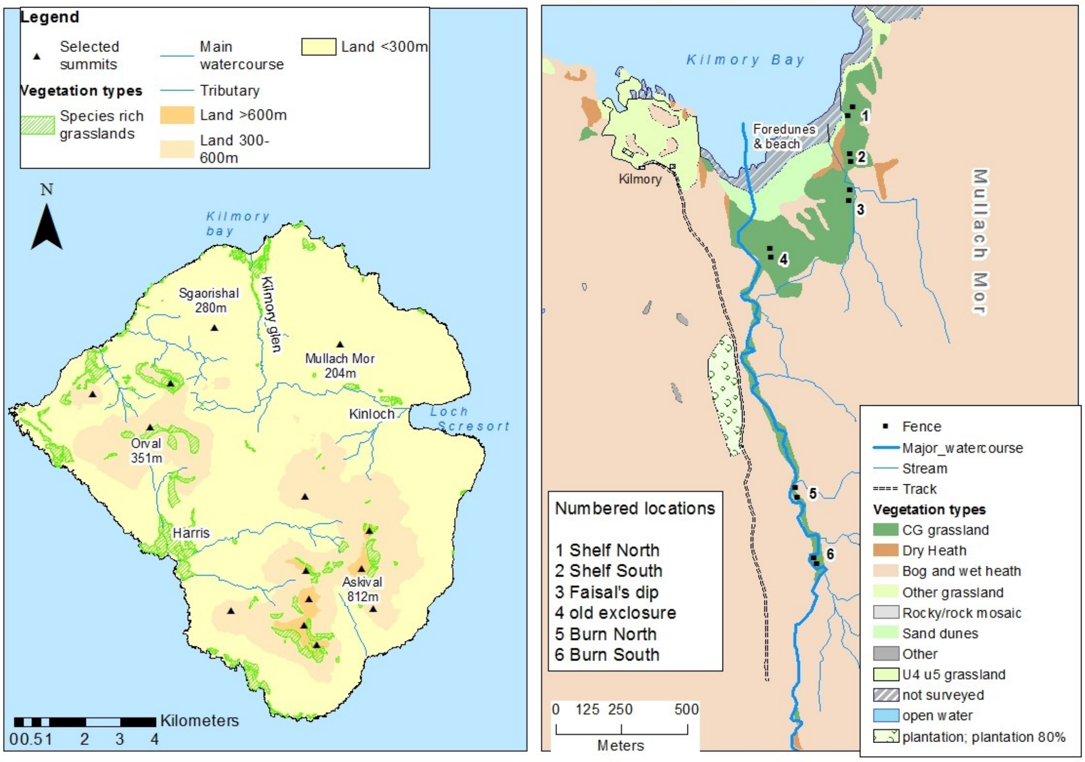

Fig 3.1: Map of location of the experimental sites (1-6) on Rum. Broad vegetation types in Kilmory glen are shown. Vegetation data derived from Bates *et al.* (2002).

Fig 3.2: The fence at site 6 in March 2011, showing the gap in two diagonally opposite corners.

3.3 Methods

Field methods

In March 2011, six experimental sites were established on species-rich grassland in Kilmory Glen (Fig 3.1) on the Isle of Rum. These grasslands are species-rich and moderately fertile. These grasslands are a priority habitat for conservation, protected under the Habitats Directive (Council of the European Communities 1992), where they correspond most closely to the grassland communities described as species-rich *Nardus* grasslands (owing to the presence of *Nardus* grass in the sward). They contain a varied mixture of other grasses and small herbs such as *Thymus polytrichus* and *Potentilla erecta* (Rodwell 1992). The grasslands occur in a very fine- scale mosaic with types of dry heath communities. These grasslands are preferred over the surrounding heaths and bog communities by grazing herbivores (Gordon 1989b). The main grazers in the area are red deer; there are also a herd of around twenty ponies which periodically graze in Kilmory glen (Pearman *et al*. 2008).

At each of the six sites a square post and wire-fenced plot of 10m x 10m and 1.2m high was erected (Fig 3.2), and a paired unfenced control plot of the same size marked out. The fenced and control plots, with centre points located between 16 and 26 m apart were matched for vegetation type as closely as possible, the choice of which plot was to be fenced at each site was random. The fences had a 45 cm wide gap at two opposite corners to allow limited access to the interior by deer; the width of the gap prevented any access by ponies. In the March 2012, the gaps were closed as the fences had not reduced grazing intensity sufficiently. In the two following years, deer could still access the fenced plot by pushing through or jumping the four wires (Fig 3.2). The fences were removed at the end of the study in August 2013 for operational reasons.

The reduction in grazing on each plot was assessed by dung counts in comparison to the adjacent control plot. Within each fenced and control area four permanent dung plots (5 m x 2 m) were established and marked with wooden pegs. Dung plots were cleared after counting, which took place in March, July and November of each year. Decay rates are unknown for the habitat and location. Where decay rates are unknown a gap of 3 months between clearance counts is considered a reasonable time period, which is likely to capture most dung deposited before it decays (Mayle *et al*. 1999). The approximately four month gap between counts in summer time this study mean that in wet weather it is likely that a small proportion of dung groups disappeared before they could be counted. Over the winter months, lower temperatures mean that decomposition is slower and the 4-5 month gap (sites surveyed mid-November and very end of March) ought to be sufficient to capture all of the dung deposited in the winter months when decomposition rates are slower. Frequency of clearance was a compromise between maximising the dung that was counted and practicalities of counting more frequently (Mitchell & McCowan 1984, Mayle *et al.* 1999). The species, number of groups of dung and the number of pellets were recorded. Dung groups were not recorded if they were too degraded for the species to be determined. As a second approach, counts of deer within the fenced and control plots were made during deer censuses carried out as part of the individual based deer study in the area (Clutton-Brock *et al.* 1982). This record was made from Jan 2012 to July 2013, five times monthly.

Experimental sites were surveyed at baseline in March 2011 and measurements repeated in every March, July and November until July 2013. All data collection methods other than dung counts were conducted a minimum of 1m from the boundary fence to avoid edge effects. In each fenced plot and corresponding control plot, the following measurements were made. Four 1m x 1m permanent botanical plots (referred to as sub plots) were established in each plot (total eight per site, four in the fence and four in the control plot) and the percentage cover of all vascular species was recorded to species level, the percentage cover of bryophytes was also recorded to species level where possible; the cover of dead material and bare ground was also recorded. A single estimate of sward height was made in each fenced and control plot, using a HFRO sward stick to take 30 measurements along a 'W' shaped transect (Barthram 1985). Utilisation of heather was measured in all plots where the species was present at >10% cover. A 1m pin drop quadrat with ten pins was used for this: the nearest stem (if there was one within 5cm) was assessed for browsing using a modified version of the method in Grant (1981). The browsing on the heather shoot closest to each point was recorded on a 3 point scale as follows. 0= unbrowsed, 1= current year's growth browsed, 2=browsed into previous years wood. A total of ten pin drop quadrats were used per plot, in total measuring up to 100 stems of heather.

Utilisation of grasses species was recorded in similar manner for any graminoid species that made up ≥10% cover (in the botanical sub-plots). For *Carex* species and *Festuca* species all species present were treated as a single category. For each pin-drop, the nearest (green) tiller or stem within a 5cm radius of the pin of each species/category was recorded as either grazed or ungrazed. *Festuca* Spp. and *Poa pratensis* were the only species recorded in most sub-plots in all time periods.

The species flowering were recorded in 40, 50 cm x 50 cm quadrats in each plot in June of all years; the identity of all flowering species in each quadrat was recorded. From this a frequency of occurrence (count out of 40 quadrats) was obtained for each species. Following initial examination of the data, it was felt that the quadrat may have been too large to capture differences in frequency of flowering between plots and sites. In 2013, therefore, an additional assessment of flowering was made using a smaller 20 x 20 cm quadrat placed 20 times within the plots. Within these smaller quadrats all flowering species were recorded and the number of flower heads per species was also counted so that both frequency and density of flower heads of a species could be obtained.

Statistical methods

Botanical species composition

Multivariate analysis of botanical composition was carried out using the vegan package (Oksanen *et al*. 2013) in R 2.15 (R Core Team 2013). The mean percentage covers of the species or categories in the four botanical sub-plots within each fenced/control plot were used for the analysis. Detrended correspondence analysis (DCA) was carried out to test whether data were suitable for linear or non-linear techniques in subsequent multivariate analysis. First axis length was 2.5SD, suggesting either linear or non-linear methods were suitable (Leps & Smilauer 2003). Linear methods were chosen. Redundancy analysis (RDA) (Van den Wollenberg 1977) was used to test for changes in species composition; the interaction between Treatment and Time (as a categorical variable) was tested. Time and Site were included as variables to account for trends over time and plot pairing. Significance testing in the RDA is by the Monte-Carlo method. Restricted permutation was imposed on the Monte-Carlo method to account for repeated measures in time. As a second approach the Cumulative Dung count (excluding baseline count) and Time were used as explanatory variables, with the same covariables and split plot design as above. The results of this latter analysis are not shown in this chapter but can be found in Appendix IV.

Univariate response variables

All other statistical analyses were carried out in R, version 2.15 (R Development Core Team 2012). The effect of the Treatment x Time interaction was tested on the mean value of a response variable in each plot (averaging over the 4 sub-plots) using linear mixed models in package nlme (Pinheiro *et al.* 2012).

The full time series was analysed using linear mixed effects models, with the random effect of site to account for the pairing. Experimental sites covered a height range of 1.1 cm to 6.4 cm at baseline (in March 2011, at the beginning of the growing season. Because starting conditions are known to affect the influence of changing grazing intensity (see section 3.1), the interaction between Treatment, Time and Starting height was tested for the following response variables: litter, bare ground, cover of graminoids, cover of herbs, Shannon diversity index, and utilisation of heather and common grasses. The effect of Treatment, Time and Starting height on the cover of the 6 most commonly occurring species of graminoid, and 10 most common herbs, and *Calluna vulgaris* was tested. All interactions up to the three-way interaction between Treatment, Time and Starting height were tested and non-significant terms sequentially dropped from a maximal model. Time and Month were always included in the model whether or not significant because the effect of season always needed to be accounted for. Percentage covers were log transformed (ln + 1) before analysis to normalise the data. Common species were chosen because it would be difficult to detect changes for rarely occurring species, given the small number of sites in the study. The species chosen were also some of the most abundant vascular plant species. Time was treated as a linear variable (number of months since baseline) and month was included as a categorical variable to account for seasonal effects. Ideally, time would have been treated as a single categorical variable, and month omitted, but due to the low replication in this study, time this was not possible as it results in over-fitting when all interactions are included.

For sward height, the interaction between Treatment and Time was tested using a nested random effect model structure: plot was nested within site, with 30 height measurements per plot.

Flowering

The effect of Treatment on the number of species flowering within each sample plot (and total number of flower heads in 20cm x 20cm quadrats recorded in 2013 only) was analysed for each year separately using linear models. Additionally the effect of Treatment on a selection of common individual species was made, to see if there was any general pattern to species response to reduced grazing.

Linear mixed effect models were used to test for differences in frequency (and number of flower-heads in 2013) between fenced and control plots. Models with frequencies as response variables were fitted using binomial link function which fits a logistic odds model. Models with count data as the response used a Poisson link function. As above, Site was included as a random effect and data from different years was analysed separately. The most commonly flowering herb and graminoid species were selected in each year to increase the power to detect differences.

3.4 Results

Reduction in grazing

Dung counts indicated that there was a reduction in grazing pressure in all plots overall (Fig 3.3). No pony dung was found inside fenced plots except that a pony got in to the ite 2 fenced plot in July 2013 which was consequently heavily grazed and not assessed on this final survey date. There was much variation in the degree of reduction in deer use as judged from dung; occupancy of fenced plots was reduced by anything between 10 and ~80% compared to control plots. Occupancy levels appear to be lower in the fenced pots when actual deer counts are used, the reduction ranging from ~30 to 90% in this case, although there were no deer recorded in either plot at site 6 (Fig 3.4). The least and most reduced sites (sites 5 and 1) are the same according to both deer and dung counts (Fig 3.3; Fig 3.4), with sites 2, 3, and 4 having intermediate reductions. The ratios of deer counts and dung counts are similar in 1 and 5, but deer counts indicate a lower rate of use than the dung counts for the most closely corresponding period at sites 2, 3 and 4. For the most closely comparable time period (dung group counts from Nov 2011-July 2013, deer counts started in January 2012) the correlation between the two measures was only 0.49.

The disparity between the deer count and dung count ratio is likely due to the sparseness of the deer count data. It is noted that at site 5 the reduction in dung count is minimal and indeed the dung count was higher inside the fence on some occasions (not shown). It was also noted that some individual deer were using this site to ruminate, thus potentially increasing the dung count disproportionately compared to actual grazing impact in this plot.

Height changes in response to reduced grazing

Control plots differed substantially in height from each other. Three of the sites (numbers 1, 2 and 4) had very short grazed swards (<5cm in the control plots in July of all years) while the other three had taller swards with mean height between 8 and 12cm in July in the control plots.

The height of the sward in the fenced plots was significantly higher than the controls in July 2011 ($p=0.0006$), and from July 2012-July 2013 ($p=<0.002$). Examination of individual plots shows that each has increased in height relative to the control by the end of the experimental period (Fig 3.5). Note that despite efforts to identify homogeneous plots within sites, some fenced plots were initially shorter than their controls.

Variation in height

The vertical structure of the plots was not measured directly, however, it can be inferred from the coefficient of variation of the sward height measurements in each plot. There was no Treatment x Time interaction effect on coefficient of variation of heights in the plots.

Species composition

There was little change in the botanical composition in response to reduced grazing**.** Redundancy Analysis (RDA) of the interaction of Treatment and Time over the whole time period was conducted. The first axis explained 3.0% of the variance and was not significant ($p=0.50$). Replacing the Treatment x Time interaction with the accumulated dung group count group resulted in a 1st axis explaining only 1.7% of the variance which was non-significant ($p=0.40$).

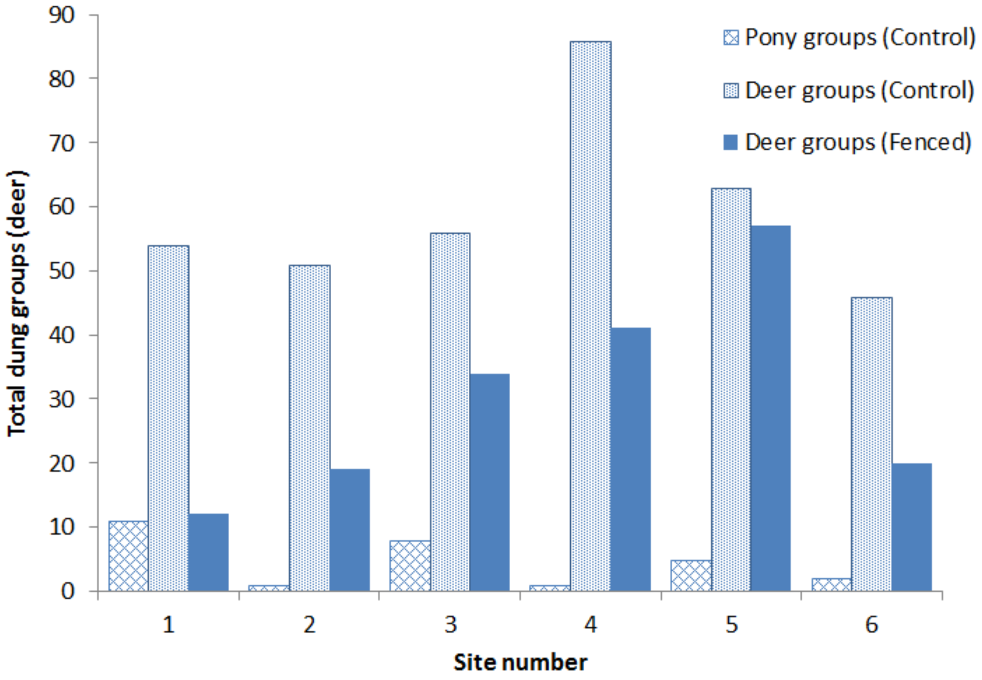

Fig 3.3: Total cumulative dung counts (deer and pony groups) across all measurement periods, excluding the baseline count, for each plot.

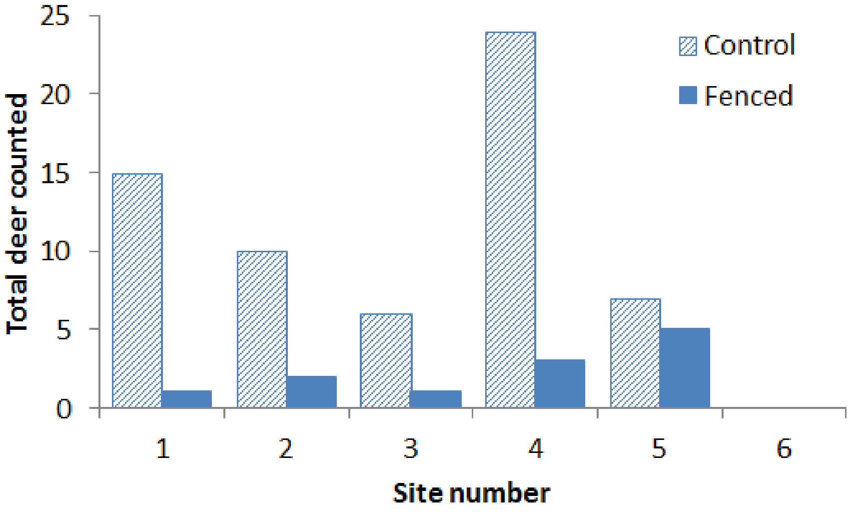

Fig 3.4: Deer counted in fenced and control plots between Jan 2012 and July 2013.

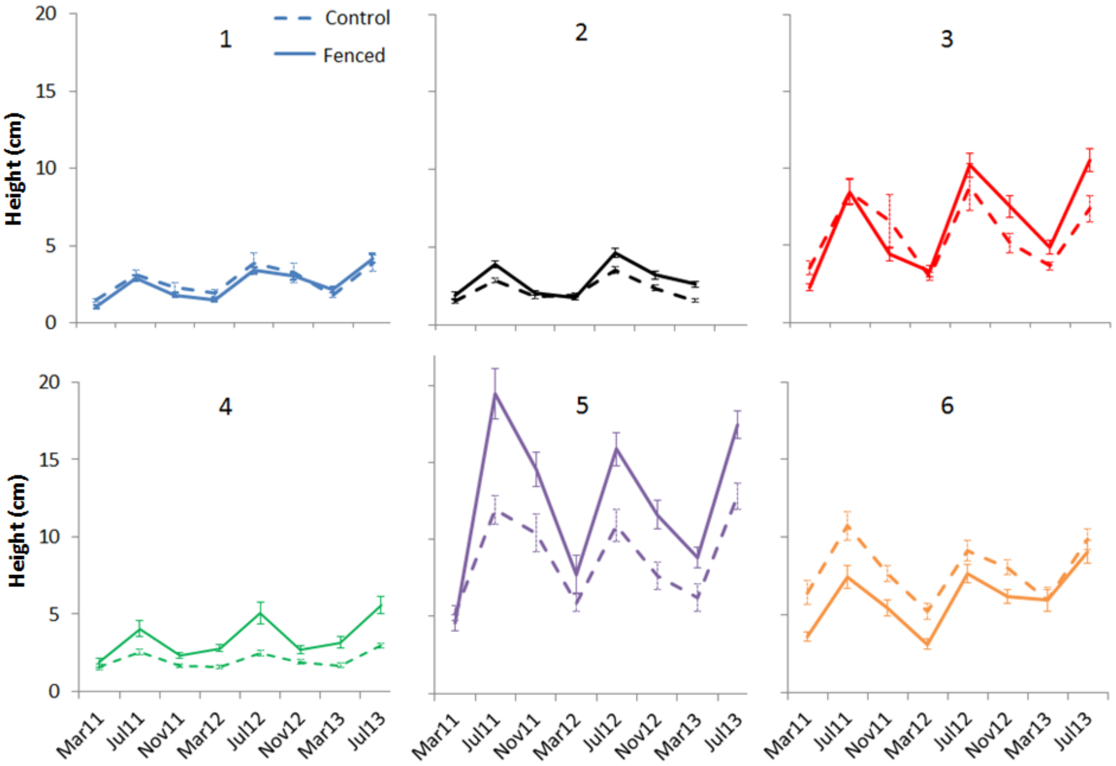

Fig 3.5 Mean sward heights of cage and control for each site. Note that some fenced plots are initially shorter than the controls, but all increase in height relative to their paired control over the course of the experiment. Error bars are 1 S.E. Note that the two shortest sward sites (1 and 2) biomass was slow to accumulate even when grazing was excluded (this is located close to the K2 group of total grazing exclusion plots in the previous chapter, which found a similar result).

Changes to cover of commonly occurring species

The percentage cover was not significantly associated with a Treatment x Time interaction for any of the 17 common species tested (Table 3.1). However, there were several significant responses involving the interaction Treatment x Starting height. This suggests that the effect of reducing grazing on some species was dependent on starting conditions. Although there were no three way interactions including time, the significant two-way interactions between treatment and start height were not due to baseline differences. Where this interaction was significant in the whole dataset, the interaction was tested for baseline data only and found to be non-significant (p>0.1) for all response variables. Treatment x Start height interaction had a significant effect on the percentage cover of three of the five grass species. *Poa pratensis* decreased more in the taller reduced grazing plots, whereas *Agrostis stolonifera* and *Anthoxanthum odoratum* increased in initially taller plots that were fenced and did not change much or decreased in shorter fenced plots (Table 3.1). There were no significant three way interactions including Time.

However, only two of the 10 herb species tested responded. The general pattern that emerges is that grasses are responding more than herbs, but the direction of the effect is dependent on initial conditions (Table 3.1).

Changes to diversity, cover of broad vegetation groups, and structural measurements

There was no significant effect of Treatment x Time interaction on diversity, species number, litter, bare ground, cover of graminoids or herbs or utilisation of *Festuca* spps ($p>0.05$). Bare ground was significantly related to the three-way interaction Treatment x Time x Starting height ($p=0.005$). Bare ground was reduced more in initially taller plots that were subject to reduced grazing (Table 3.2).

Herb cover, graminoid species cover and litter cover were all significantly related to the interaction between Starting height and Treatment. There was less herb cover, a higher number of graminoid species and a higher litter cover in the fenced plots which were taller at the beginning of the experiment (Table 3.2). This suggests the effect of treatment on these parameters is dependent on initial conditions.

There were few relationships between accumulated dung counts and diversity, species number, litter, bare ground, cover of graminoids or herbs (results shown in Appendix IV). The only significant result was less graminoid species in plots with a higher dung count, and it was only just significant ($0.01<p<0.05$).

Table 3.1: The response of common plant species to Treatment and Starting height. Final models from the maximal model y~ Treatment * Time* Start height + month are shown only where interaction(s) including the effect of treatment are present. Species with no effect of Treatment are listed without model results. Only significant interactions and main effects are shown. Time is included as a numeric vector, so month is also included to account for seasonal effects. Time = time in months since the start of the experiment. Fence = effect of reduced grazing (compared to control). Start Ht = mean height in March 2011 in cm.

Species	**Significant effects**	**Coefficient**	**Std Error**	**p-value**
Poa pratensis	Intercept	2.80	0.302	
	March (vs July)	0.252	0.128	0.052
	Nov (vs. July)	0.383	0.141	0.008
	Time	-0.014	0.006	0.024
	Fence (vs control)	0.669	0.248	0.009
	StartHt	-0.196	0.070	0.006
	Fence x StartHt	**-0.340**	**0.086**	**0.0002**
Agrostis stolonifera	Intercept	-0.310	0.322	
	March (vs July)	-0.254	0.163	0.123
	Nov (vs. July)	-0.315	0.180	0.084
	Time	0.015	0.016	0.350
	Fence (vs control)	-0.477	0.307	0.125
	StartHt	0.410	0.084	<0.0001
	Time x StartHt	$-9.25e^{-3}$	0.005	0.048
	Fence x StartHt	0.324	0.099	**0.0016**
Anthoxanthum odoratum	Intercept	0.905	0.220	
	March (vs July)	-0.682	0.125	<0.001
	Nov (vs. July)	-0.480	0.138	0.001
	Time	0.007	0.006	0.243
	Fence (vs control)	-0.354	0.238	0.141
	StartHt	0.0139	0.048	0.775
	Fence x StartHt	0.171	0.078	**0.031**
Thymus polytrichus	Intercept	1.66	0.375	
	March (vs July)	-0.676	0.115	<0.0001
	Nov (vs. July)	-0.475	0.128	0.0004
	Fence (vs control)	1.14	0.232	<0.0001
	StartHt	-0.064	0.083	0.452
	Fence x StartHt	**-0.366**	**0.086**	**0.0001**
Lotus corniculatus	Intercept	0.322	0.104	
	March (vs July)	-0.334	0.050	<0.0001
	Nov (vs. July)	-0.351	0.056	<0.0001
	Fence (vs control)	0.226	0.097	0.023
	StartHt	0.019	0.025	0.445
	Fence x StartHt	**-0.071**	**0.033**	**0.037**

Species with no significant relationship to Treatment interactions. *Carex flacca; Luzula campestris; Calluna vulgaris; Festuca rubra; Plantago lanceolata; Plantago maritima; Potentilla erecta; Prunella vulgaris; Trifolium repens; Succisa pratensis*

Changes to utilisation of heather and grasses

The recorded level of browsing on *Calluna* was highest in March 2012, with between 50 and 61% of shoots browsed (Control mean 53%, fenced mean 57%). In March 2013 the *Calluna* utilisation was still high in both fenced (mean 38%) and control plots (mean 51%) with the total range for all plots being 33 - 56% browsing. There was a significant effect of Treatment x Time interaction on *Calluna* utilisation, there was less browsing in reduced grazing plots (p=0.014) (Table 3.2). Mean browsing levels on *Calluna* began to diverge between treatments in July 2012. There was no significant effect of Treatment x Time on *Festuca* utilisation (Table 3.2). There was no relationship between accumulated dung count within the growing season and utilisation of *Calluna* or *Festuca*.

Effect on number of species flowering and flower density.

There was a greater number of both herb and graminoid species flowering in the fenced plots than the control plots in 2011 and 2012 (Table 3.3). The difference was only significant for herbs. In 2013, there were no significant differences in either the overall number of species flowering or in the number of graminoid or herb species flowering. Data from the 20 x 20 cm plots (2013 only) showed that there was a higher average flower density in the fenced plots (Table 3.4) however, the difference was not significant.

Individual species

For most species, there was no significant difference in flowering between fenced and control plots. For graminoids, the general pattern was that there was increased in frequency in the fenced plots (Table 3.5). There was one exception to this rule, the density of flowerheads of *Cynosurus cristatus*, a species that is generally promoted by heavy grazing and bare ground (Bullock *et al.* 1995), was significantly lower in fenced plots in 2013. A high proportion of herb species differed significantly between treatments in 2011 and 2012. There is no general pattern in direction of herb species response (Table 3.5: Table 3.6), and in some cases the same species responded differently in different years.

Table 3.2: The effect of the treatment, time and starting height on various response variables. Models shown below are final models after stepwise deletion of non-significant interactions and main effect terms under ML fitting, excepting that month always remained in the model as a main effect. Coefficients are those when model is fitted using REML. Response variables whose final models had no significant interactions involving treatment are listed at the bottom of the table with no model details. StartHt=starting height of plot (cm); Time=time from March 2011 in months; Fence= Effect of fencing compared to control plots

Response	**Significant variables**	**Coefficient**	**Std. Error**	**p-value (ML)**
Log(Litter)	Intercept	1.06	0.250	
	March (vs July)	1.70	0.147	
	Nov (vs. July)	1.17	0.162	
	Time	0.020	0.004	
	StartHt	0.014	0.055	
	Fence (vs. Control)	-0.503	0.278	
	StartHt x Fence	0.206	0.091	**0.025**
Log(Bare ground+1)	Intercept	-0.355	0.658	
	March (vs July)	0.533	0.178	
	Nov (vs. July)	0.211	0.196	
	Time	-0.002	0.011	
	StartHt	-0.272	0.152	
	Fence (vs. Control)	-1.15	0.614	
	Time x StartHt	0.005	0.003	
	Time x Fence	0.028	0.018	
	StartHt x Fence	0.322	0.208	
	Time x StartHt x Fence	-0.016	0.006	**0.008**
Graminoid species number	Intercept	14.1	1.07	
	March (vs July)	-4.05	0.389	
	Nov (vs. July)	-4.33	0.429	
	Time	0.028	0.009	
	StartHt	0.122	0.243	
	Fence (vs. Control)	-1.67	0.764	
	StartHt x Fence (vs. Control)	0.749	0.274	**0.006**
Log(Herb cover)	Intercept	3.49	0.292	
	March (vs July)	-1.21	0.115	
	Nov (vs. July)	-1.12	0.128	
	StartHt	-0.13	0.070	
	Fence (vs. Control)	0.688	0.228	
	StartHt x Fence (vs. Control)	-0.252	0.081	**0.003**
Calluna utilisation	Intercept	6.41	3.52	
	March (vs July)	33.3	2.59	
	Nov (vs. July)	22.2	2.85	
	Time	0.243	0.087	
	Fence (vs. Control)	2.65	3.99	
	Time x Fence	-0.295	0.123	**0.021**
Poa utilisation	Intercept	0.197	0.039	
	March (vs July)	0.001	0.024	
	Nov (vs. July)	0.212	0.025	
	Time	0.001	0.001	
	Fence (vs. Control)	0.026	0.037	
	Time x Fence	-0.002	0.001	**0.034**
Other response variables tested:				
Festuca spps utilisation; Herb species number; Log(Graminoid cover); Shannon diversity index				

Table 3.3: Mean number of species flowering per plot, using the data from the 40x40cm flowering quadrats. P-values of differences are from an ANOVA with treatment as the fixed effect and Site as the random effect. There were no interactions with sward height.

Year	**Treatment**	**Mean number of species flowering**					
		All species	**S.E.**	**Graminoids**	**S.E.**	**Herbs**	**S.E.**
2011	**Control**	24.2	1.05	10.67	1.61	14.6	1.12
	Fenced	26.3	0.333	11.00	0.82	16.3	1.35
	F	**F=9.423**		F=0.357		**F=8.939**	
	d.f.	1,5		1,5		1,5	
	p-value	**0.028**		0.576		**0.031**	
2012	**Control**	27.8	2.04	13.3	1.26	14.5	1.15
	Fenced	32.5	0.619	15.0	1.18	17.5	0.922
	F	**F=14.41**		F= 2.66		**F=9.00**	
	d.f.	1,5		1,5		1,5	
	p-value	**0.013**		0.164		**0.030**	
2013	**Control**	30.6	2.23	15.4	1.36	15.2	2.22
	Fenced	31.0	1.10	15.2	0.86	15.8	1.59
	F	F=0.11		F= 0.038		F= 0.419	
	d.f.	1,4		1,4		1,4	
	p-value	0.757		0.854		0.553	

Table 3.4: Total flower head number counted in all 20 of the 20 x 20 cm quadrats used at each plot to assess flowering in 2013. P-values of differences are from an ANOVA with treatment as the fixed effect and Site as the random effect.

		Number of flowerheads		
Site	**treatment**	**Total**	**Graminoids**	**Herbs**
1	**C**	312	32	280
1	**F**	417	58	359
3	**C**	259	167	92
3	**F**	558	165	393
4	**C**	283	111	172
4	**F**	301	165	136
5	**C**	342	226	116
5	**F**	166	109	57
6	**C**	341	80	261
6	**F**	353	85	268
Average	**C**	**307.4**	**123.2**	**184.2**
	F	**359**	**116.4**	**242.6**
SE	**C**	16.26	33.78	37.67
	F	64.66	21.42	64.27
P-value of difference		0.539	0.827	0.420

Table 3.5: Significance testing on individual species flowering frequency as recorded in the 50cm x 50cm quadrats in relation to partial fencing. The most common species were selected (those flowering in at last 11 plots in 2011, 2012 and at least 9 in 2013) $^{+}$= p 0.1-0.05; *= p<0.05; **=p<0.01; ***= p<0.001.

Year	Species	Coefficient of fencing (vs. control)	Std Error	P-value
2011	*Anthoxanthum odoratum*	-0.309	0.197	0.117
	Cynosurus cristatus	0.044	0.210	0.833
	Danthonia decumbens	**0.473**	0.223	**0.034***
	Festuca ovina/vivipara	-0.090	0.212	0.699
	Koeleria macrantha	0.356	0.194	0.066^{+}
	Plantago lanceolata	**1.26**	0.247	**$3.04e^{-7}$ *** **
	Plantago maritima	**0.870**	0.238	**$3.00\ e^{-4}$*** **
	Polygala vulgaris	0.443	0.244	0.0687^{+}
	Potentilla erecta	**-0.448**	0.212	**0.035***
	Prunella vulgaris	**-0.520**	0.214	**0.015***
	Trifolium repens	0.457	0.317	0.151
2012	*Agrostis stolonifera*	**1.79**	**0.258**	**$3.79e^{-12}$ *** **
	Anthoxanthum odoratum	**1.63**	**0.242**	**$1.83e^{-11}$ *** **
	Festuca ovina/vivipara	0.406	0.316	0.199
	Cynosurus cristatus	-0.324	0.208	0.120
	Danthonia decumbens	-0.337	0.212	0.113
	Koeleria macrantha	0.177	0.188	0.347
	Potentilla erecta	-1.38	0.229	0.644
	Plantago maritima	**-0.444**	0.206	**0.031***
	Plantago lanceolata	**0.815**	0.271	**0.003****
	Prunella vulgaris	**-0.997**	0.189	**$1.4e^{-7}$ *** **
	Thymus polytrichus	**-1.175**	0.219	**$1.44e^{-15}$ *** **
	Trifolium repens	**1.31**	0.262	**$5.95e^{-7}$ *** **
2013	*Anthoxanthum odoratum*	0.475	0.242	0.055^{+}
	Agrostis stolonifera	**0.577**	**0.226**	**0.011***
	Holcus lanatus	-0.036	0.265	0.893
	Festuca ovina/vivipara	0.202	0.282	0.473
	Carex pulicaris	**1.03**	**0.255**	**$4.97e^{-5}$*** **
	Cynosurus cristatus	-0.342	0.214	0.110
	Danthonia decumbens	-0.111	0.235	0.636
	Koeleria macrantha	0.156	0.227	0.493
	Luzula campestris	-0.418	0.264	0.114
	Plantago lanceolata	0.075	0.372	0.782
	Plantago maritima	-0.142	0.238	0.550
	Polygala vulgaris	**0.733**	**0.248**	**0.0008*****
	Prunella vulgaris	-0.385	0.202	0.0568^{+}
	Trifolium repens	**0.851**	**0.314**	**0.0068****

Table 3.6: Significance testing on differences in frequency and number of flower heads recorded for individual species in the 20cm x 20cm quadrats, 2013 only. Frequencies fitted using binomial link function which fits a logistic odds model. Count analyses use Poisson link function. $^{+}$= p 0.1-0.05; *= p<0.05; **=p<0.01; ***= p<0.001.

	Species	**Effect fencing**	**Std Error**	**P-value**
Frequency	*Anthoxanthum odoratum*	0.920	0.746	0.200
	Agrostis stolonifera	0.159	0.394	0.686
	Cynosurus cristatus	-0.542	0.349	0.120
	Koeleria macrantha	0.372	0.383	0.331
	Festuca vivipara	0.107	0.325	0.735
	Potentilla erecta	$-4.63e^{-6}$	0.405	0.999
	Plantago lanceolata	**-1.30**	**0.467**	**0.0024****
	P. maritima	**-1.04**	**0.372**	**0.0005*****
	Prunella vulgaris	-1.05	0.408	**0.010***
	Thymus polytrichus	0.110	0.330	0.739
Count	*Anthoxanthum odoratum*	$-2.57e^{-6}$	$1.73\ e^{-1}$	0.999
	Agrostis stolonifera	-0.3054	0.245	0.221
	Cynosurus cristatus	**-0.581**	**0.215**	**0.0069*****
	Koeleria macrantha	0.392	0.355	0.124
	Festuca ovina/vivipara	-0.396	0.168	0.078^{+}
	Potentilla erecta	0.134	0.255	0.600
	Plantago lanceolata	**-0.377**	**0.108**	**0.0005 *****
	Plantago maritima	**-0.636**	**0.154**	**$3.39e^{-5}$*****
	Prunella vulgaris	**-1.04**	**0.351**	**0.0032****
	Thymus polytrichus	-0.041	0.101	0.684

3.5 Discussion

Using semi-permeable fencing proved successful in reducing grazing levels on small areas and is a viable alternative to more costly methods in studying the effects of reduced grazing. There were significant changes in sward height over the three years; however, this did not cause a significant shift in species composition. The results of previous experiments on other grassland types (related in species composition but less species rich) suggest that the magnitude of the height change would have been sufficient to affect vegetation composition in the longer term (Grant *et al*. 1996b, Hulme *et al*. 1999, Holland *et al*. 2008). Flowering increased in the first two years in fenced plots but few other parameters of the vegetation community or individual species responded to reduced grazing. There was a lot of variation in the level of reduction in grazing, but the reduction in grazing was not related to any change in the vegetation community. There were several indications that the starting vegetation structure influenced the response to reduction of grazing. Heterogeneity in starting conditions needs to be considered when assessing the potential consequences of changes in grazing regime.

Grazing reduction

Observations of deer grazing in fenced and control plots were sparse, while dung counts provided more data. The two methods of quantifying grazing reduction did not correlate especially well. Both methods did, however, show a reduction in grazing inside all of the fenced areas compared to paired controls.

Vegetation response to grazing reduction and effect of starting height

The response of community composition to Treatment was not significant. This lack of response was probably due to the short time period of the study. It is common for changes in species composition in response to reductions in grazing intensity to take several years before becoming noticeable (Hulme *et al.* 1999, Austrheim *et al.* 2008). Even under total exclusion, botanical changes can take many years to emerge and stabilise (Rawes 1981, Hill *et al.* 1992). Responses appear to be species-specific and when the same species was tested in more than one year, they were rarely consistently significant. In all cases where graminoids responded to Treatment, it was with an increase in frequency of flowerheads. There was no such general pattern amongst herb species. Changes in flowering could lead, in the longer term, to changes in species composition. However, the concurrent decrease in bare ground would limit sites for germination, so those species that increased flowering rates would only benefit if some bare ground remained.

Broad functional groups (graminoids and herbs), litter accumulation and species diversity were not significantly affected by Treatment. Browsing on heather decreased in frequency in the fenced plots over time, but remained high enough that the species is unlikely to increase in abundance (Pakeman & Nolan 2009).

Sward height significantly increased in the fenced plots, but structural heterogeneity, as measured by the coefficient of variation in height, was unaffected by the fencing treatment. Height changes of a similar magnitude to the ones generated in this experiment have been found to cause significant shifts in species composition on upland grassland (species poor *Nardus stricta* grassland and also *Agrostis –Festuca* grassland, though far less species-rich than that found here) within three to seven years (Grant *et al.* 1996b, Hulme *et al.* 1999, Holland *et al.* 2008), so the degree of reduction in grazing established by the fences is considered to be sufficient to induce vegetation change in the longer term.

There were some indications that community composition response to treatment depended on Starting height, although overall species composition did not change significantly, the interaction between Treatment and Starting height had a significant effect on the percentage cover of several common species. The low replication in this study limited the ability to pick up complex interactions.

The effect of the interaction between Starting height and Treatment on several parameters, indicated a stronger shift towards a grassier sward with more litter in taller plots and a weaker or reverse response in shorter plots. Starting conditions appeared to be more important than the degree of reduction in grazing in modifying response. No response variables were linked to the differences in dung density between control and reduced grazing plots (results shown in Appendix IV).

Reducing grazing on these grasslands would make already taller areas more vulnerable to invasion by species such as *Calluna* and *Molinia*, both of which are widespread and abundant in the Kilmory Glen area and adjacent to species-rich grassland. Not enough is known about the responses of this grassland type to different grazing levels to predict long term response to changes in sward height of the degree seen here. In a previous study on *Agrostis –Festuca* grassland (but a more species poor sward than in this study), maintenance of the sward at 4.5 cm in similar grasslands decreased the cover of competitive grasses compared to grazing by sheep at a sward height of 6 cm, and caused decline of *Calluna* where present (Hulme *et al.* 1999); this suggests that increasing sward height beyond 5 or 6 cm is undesirable on such grasslands, if the goal is to create conditions suitable for a high cover of herbs and to minimise shrub cover, as is often the case for grassland conservation.

Conversion to woodland is unlikely in the Rum scenario, despite a seed source in the vicinity. Long term exclusion plots in close proximity to the sites saw very little establishment of tall woody species after 50 years (Virtanen *et al.* 2002). Two birch seedlings were noted at one site in this study in May 2012, which was approximately 800m NE from the nearest seed source, but these had disappeared by the time of the July 2012 survey.

Possible application of semi-permeable fencing as a tool in reduced grazing experiments – advantages and drawbacks compared to conventional methods

The novel method of partial fencing successfully reduced grazing and did not result in total grazing exclusion; dung counts and observations showed that deer had accessed all fenced areas within the first few months of establishment. Likewise, after the gaps were closed, deer learned to access the fenced plots relatively quickly; at two sites deer were observed inside fences within two months of the gaps being closed. The sparseness of deer observations and dung count data do not allow for accurate estimation of how long this hypothesised learning period is. Three months after closing the gaps, no dung was recorded from any fenced plot, but since there were also zero dung counts for several control plots, this was more likely due to variation in deposition than a long period being required to re-habituate and learn to access the fence - at two sites, deer had been observed inside within that time period. The fences provide a filter for a sub-set of the population; it was noted that one individual was responsible for half of the observations of deer inside fences.

Semi-permeable fences could be used with livestock under the original design, with narrow entrances, however, there is a danger that habituation would occur and animals would learn where the entrances were resulting in no effective reduction of grazing in the longer term. In this study, the entrances were closed after the first year as the degree of reduction in grazing appeared to be slight, and the time period for monitoring change was restricted to three years. Although closed fences, with no entrances, allowed continued access for red deer, they might not be effective for other livestock.

There is a need for more long-term studies of moderating grazing levels on grassland, highlighted in a review by Marriott *et al*. (2004). The short term of operation of many studies on reduced grazing is currently a major limitation in studying the consequences of changes; low levels of replication are also a problem (Marriott *et al*. 2004). Studies of 3-5 years frequently find little or no change in species composition, certainly it is not expected that vegetation changes will have stabilised over this time. The main advantages of the semi-permeable fence method over more conventional adjustment of stocking rates or culling of wild deer is the lower cost of fencing small areas compared to maintaining areas of different grazing intensities over a long study period. It would be recommended that fences are maintained for much longer periods than here, ideally decades, to allow changes in vegetation to develop more fully. The small size should also make high replication possible.

A drawback of the fencing design is that there is no direct control over the degree of reduction of grazing. This is countered to some extent by the system having flexibility to easily add up to four corner entrance points, or add additional strands of wire. We chose to use dung counts as a simple measure of grazing reduction. Direct observations would have to be more frequently or intensively made in order to be useful, which would increase labour intensity of the method. Unsurprisingly, and despite the high deer density on the grasslands, total dung counts in experimental sites were low due, possibly due to their small area. The time interval between counts in this study was longer than optimal for the climatic region and habitat type, but given the very low numbers of dung pellet groups, increasing the frequency of counts would be unlikely to make a substantial difference in our ability to accurately calculate reductions in density. It would be possible to increase the size of fence, but this would be limited by the need for increased spacing between fences to avoid substantially increasing the utilisation of areas between fences. Also, fenced areas need to be small enough that deer (or other species) do not simply spend the whole day grazing inside them, in which case they might increase rather than decrease the intensity of grazing.

For larger scale studies, if grazing reduction was carried out over multiple grasslands, each with several fenced grazing reduction plots, grazing reduction could be estimated across the grassland by totalling counts from all experimental plots for cross comparison between grassland areas. But for small scale studies like the one here, it is suggested that except in cases where the initial density is very high, it may not be possible to accurately quantify the reduction in grazing by the dung count method. Certainly any seasonal variation in the differences in grazing intensity would not easily be detected. An alternative means of quantifying grazing reduction would be to measure proportion of biomass offtake by having a smaller exclusion plot inside and outside of each fence, or to use differences in standing biomass between fenced and control areas as a metric.

Conclusions

Responses to changes in grazing pressure on species-rich semi-natural grassland is known to be highly site dependent and simply setting a certain sward height or animal density will not produce the same results in all areas (e.g. Hulme *et al.* 1999, Scimone *et al.* 2007, Dumont *et al.* 2012).

The main results of this study were to show that response to partial reduction in grazing intensity by wild red deer over three growing seasons resulted in changes to sward height, but not structural heterogeneity, or community composition. There were only slight changes to cover of broad functional groups and common species following grazing reduction, and these changes depended on initial conditions. The reduction in grazing led to clear increases in flowering, particularly of graminoids, which may provide a mechanism of future community compositional change over a longer period than this experiment. However, the reduction in bare ground with decreased grazing will reduce the net contribution of seedling establishment to community change.

If conservation targets for grassland condition are based on heights, then these may be modified by relatively minor partial reduction in grazing intensity. The method devised here provided a possible means of inducing such change in order to assess the consequences for grazing reduction. The consequences of reduction in deer numbers would be highly dependent on changes in the spatial distribution of grazing, which will be dependent on pre-existing vegetation patterns (Adler *et al.* 2001, Scimone *et al.* 2007).

Although it does not match the ideal situation of a large- scale, long term study, well replicated with a standard methodology (Marriott *et al.* 2004, Garnier *et al.* 2007), small scale fencing represents a viable option for longer term study when funding for a larger scale study is unlikely. The low cost means the possibility of extending the study, possibly for several decades, is more likely to be viable, allowing assessment of changes over a much longer time period. The problem of assessing the amount of grazing reduction can be overcome by using biomass offtake or differences in standing crop as a metric. If the pace of vegetation change is slow, monitoring of botanical changes might only need to be carried out every few years, although monitoring of utilisation levels (whether by dung counts, biomass offtake or some other metric) would need to be carried out more frequently.

Chapter 3b: Implications of experimental results (3a) for conservation management of upland calcareous grasslands

3.6 Introduction

Many types of grassland are of conservation value for their plant species, associated insect fauna or aesthetic value. Recent land use change has threatened many areas of grassland with high conservation value in the EU. Of the remaining area, much is considered to be in poor condition (Moser & Ellmauer 2013). Light to moderate grazing on grasslands is often beneficial to conservation goals (Hobbs & Huenneke 1992, Rosenthal *et al.* 2012). Beyond this generality however, the range of grazing intensities that are appropriate can be very site dependant as it will also depend on other factors such as the species of grazer and site productivity (Rook *et al.* 2004, Cingolani *et al.* 2005). Site-specific responses to changes in grazing pressure can result in difficulties in predicting the consequences of a particular grazing regime for conservation goals, as the effects of some of these complicating factors are not yet well understood (Rook *et al.* 2004, Scimone *et al.* 2007). High levels of spatial variation in grazing pressure can add to the difficulties of assessing a site and recommending a suitable grazing regime.

Conservation of grasslands: importance and management

Many types of grassland are of conservation significance as they support rare plant species, rare assemblages of plants, or are essential habitat for threatened or endangered fauna (Bignal & McCracken 1996, McCracken & Huband 2005). These are natural or semi-natural communities, often originating under a long history of extensive agriculture, including grazing at moderate stocking densities, cutting for hay and rotational cropping. Maintaining high levels of plant diversity, especially of characteristic species, is often part of the conservation goals for species-rich grassland. The intermediate disturbance hypothesis predicts that the diversity of ecological communities will be highest at some intermediate level of disturbance rather than at the extremes of no or very high levels of disturbance (Fox & Connell 1979). This is borne out for many species-rich grasslands where grazing by large herbivores are the ‘disturbance’: both very high levels of grazing and abandonment of grazing threaten the diversity of such grasslands (Hobbs & Huenneke 1992, Cingolani *et al.* 2005). Within the EU, changes to farming practices threaten these grasslands, and large areas have already been lost over the last half century (Petit & Elbersen 2006, Renwick *et al.* 2013). In lowland, productive areas, grassland use has been intensified, leading to loss of diversity. In areas more economically marginal for farming, often traditionally used for extensive grazing, the trend is towards abandonment of farmland, with uncertain consequences for the biota (Rural Policy Centre 2008, McCracken 2011, Renwick *et al.* 2013). Changes to numbers of wild herbivores (principally deer species) will also affect the eventual outcome. High numbers of wild herbivores can threaten conservation goals (Gordon *et al.* 2004, Mysterud 2006), but in areas where farmland has been abandoned, an increase in wild herbivore numbers can functionally replace domestic grazers and maintain communities of conservation value that originated under agricultural conditions (Schutz *et al.* 2003).

Monitoring of conservation status

Priority vegetation communities for conservation described in Annex 1 of the EU Habitats Directive (Council of the European Communities 1992) have their condition assessed at regular intervals. In the UK this reporting is based on a set of Common Standards Monitoring guidelines and the assessment is used to guide future management decisions (JNCC 2004). Setting common standards ensures the condition of habitats are assessed in a comparable way across the country (JNCC 2004).

Difficulties in making management recommendations can arise where communities that have different grazing requirements occur adjacent to one another (Holland *et al.* 2010). Variation of grazing within a community type over short distances, giving rise to variation in vegetation condition can also lead to difficulties in recommending management changes. For several Annex 1 grassland types, both under and over grazing (see Chapter 1 for definitions) are reported as threats at the same site (JNCC 2012a, 2013a).

Aims

The experiment described in Chapter 3a (above) was designed to determine the short term effects of reducing but not excluding grazing from a semi-natural, species-rich grassland of high conservation value. The grassland is species-rich *Nardus* grassland, present in a mosaic with heath communities. Both heath communities and grasslands have been reported in recent surveys to be overgrazed in parts of their range at this site (Dayton 2008, Dayton 2011). Under-grazing has also been reported for the grassland (Dayton 2008, Britton & Pakeman 2009, Dayton 2011). Here the experimental results (described more fully in Chapter 3a) are compared to the criteria used to assess grassland condition in relation to grazing impacts. The implications of this for possible management options are discussed.

3.7 Methods

Study site

The study site was Kilmory Glen, Isle of Rum 57° 02' 50" N 6° 21' 00" W. The study site and methods for data collection are described in full in Chapter 3a.

The area of grassland in the study area corresponds to the protected Annex 1 habitat type 'Species-rich *Nardus* grassland' and is thus protected under EU legislation. As it is a SSSI and a SAC the condition of this and all other protected habitats on the reserve are assessed at regular intervals, based on nationally set criteria. In the most recent assessment, in 2010, of the seven species-rich grassland sites that were surveyed, one failed for 'under-grazing' and six failed for 'overgrazing' (Dayton 2011). Excessive browsing was also cited as the reason for poor condition of adjacent heath communities (Dayton 2011). If the interpretation of the reasons for grassland condition is correct, reduction of grazing should be beneficial to the condition of heath and to at least some of the grassland.

Comparison to Site Condition Monitoring

The dataset collected from the reduced grazing experiment detailed in the previous part of this chapter (3a) contains several measurements that are comparable to the attributes assessed when a Site Condition Monitoring (SCM) exercise is carried out (JNCC 2009). So far as possible, data from the reduced grazing experiment were compared with Common Standards Monitoring (CSM) criteria (JNCC 2009). I assessed how well the experimental and control plots met the criteria, and whether grazing reduction has a positive or negative effect on the fit of these grassland plots to SCM standards.

Some of the measures are only partially comparable, for example when they are measured on a different plot size than recommended in the SCM. Table 3.7, below, summarises the SCM criteria and indicates where it was possible to compare measurements from the experimental and control plots in the reduced grazing experiment with SCM criteria. Data was collected in March, November and July, but only the data collected in July are used for this comparison, as the SCM is supposed to be carried out between June and August (JNCC 2009).

Where directly or partially comparable, the data from both the control and experimentally manipulated plots were compared to the relevant SCM target and it was determined whether or not the site would pass or fail to meet the target in an assessment.

Change over time in these indicators was assessed using linear mixed models with the fixed effects including all two and three way interactions between Treatment * Time * Starting height and the random effect of Site, to account for the pairing of control and reduced grazing sites. Reference is made to relevant results of analyses detailed in the previous section.

Table 3.7: SCM criteria for condition of Calcareous grassland in upland areas, including Species-rich *Nardus* grassland on siliceous substrates in montane areas (JNCC 2009). Comparability to experimental data.

SCM assessment criteria	**Assessment method in SCM**	**Comparable measurement made in reduced grazing experiment?**	**Assessment method in reduced grazing experiment**
Two indicator species (of those listed in Table 3.8**)**	Visual. Per 1 x 1m	Yes	Visual 4 x 1 x 1m^2 plots
Vegetation composition 1. 33% *Dryas* or herbs 2. < 1% non-native species 3. <10% bracken or scattered native trees/shrubs 4. <25% *Bellis* and *Ranunculus repens* in total 5. <1% collectively of species in Table 3.9 6. < 10% cover *Juncus effusus*	Visual: Numbers 1, 4, 5, 6 at 1 x 1m and 2, 3, 5, 6 all visible area	Yes for 1,4, Partial 5,6, 2,3	Visual Four 1 x 1m plots Measurements not made at all visible area scale
Height 25% or more >5cm, 25% or more < 5cm.	1 x 1m^2 scale Excluding graminoid flower-heads	Partial	30 measurements at 10m^2
Litter thatch <10%	1 x 1m	Partial	Litter measurement at 1 x 1m includes standing dead material so will be an over-estimate.
Disturbed bare ground <10%	2 x 2 m And visible area	Partial	Bare ground measured at 1 x 1 m. Not assessed for whether 'disturbed' or not, so will be an overestimate compared to CSM assessment.

Table 3.7 cont. SCM criteria for condition of Calcareous grassland (upland, including Species-rich *Nardus* grassland on siliceous substrates in montane areas) (JNCC 2009), comparability to experimental data.

SCM assessment criteria	**Assessment method in SCM**	**Comparable measurement made in reduced grazing experiment?**	**Assessment method in reduced grazing experiment**
Indicators of grazing **At least half of statements (a) to (f) should be true** a) Less than 10% of grass and sedge tillers uprooted. b) Less than 10% of live leaves with signs of having been grazed for any of *Alchemilla alpina, Nardus stricta, Prunella vulgaris, Sibbaldia procumbens, Thymus polytrichus.* c) Less than 50% of live leaves of legumes or *Plantago lanceolata* with signs of having been grazed. d) Less than 66% of live leaves of grasses with signs of having been grazed. e) Less than 25% broken or uprooted (any of) *Huperzia selago, Minuartia sedoides, Saxifraga hypnoides, Selaginella selaginoides, Silene acaulis.* f) More than 50% of the shoots of Dryas at least 3 cm long.	1 x 1m	Partial for d). No comparable measurements for a, b, c, e or f	Proportion of live grass leaves grazed measured for main grass species only, at 10 x 10m scale

Table 3.8: Indicator Species for Species-rich *Nardus* grassland (which includes CG10 *Festuca ovina-Agrostis capillaris-Thymus polytrichus grassland* (not on limestone), CG11 *Festuca ovina-Agrostis capillaris-Alchemilla alpina grass-heath* (not on limestone), U4 - *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland (species-rich types), U5c *Nardus stricta-Galium saxatile Carex panicea-Viola riviniana* sub-community). Taken from (JNCC 2009), plant community names from (Rodwell 1992)

Indicator Species for Species-rich *Nardus* grassland — CG10 (not on limestone), CG11 (not on limestone), U4 (species-rich types), U5c

Alchemilla alpina
Alchemilla glabra
Angelica sylvestris
Briza media
Campanula rotundifolia
Carex caryophyllea
Carex panicea
Cerastium fontanum
Danthonia decumbens
Filipendula ulmaria
Galium verum
Geum rivale
Lathyrus linifolius
Lotus corniculatus
Pinguicula vulgaris
Persicaria vivipara
Stachys officinalis (S. betonica)
Succisa pratensis
Thymus polytrichus

Table 3.9: Undesirable species for species-rich *Nardus* grassland. Taken from (JNCC 2009)

Undesirable species

Arrhenatherum elatius
Cirsium arvense
Cirsium vulgare
Cynosurus cristatus
large docks (excluding *Rumex acetosa*)
Lolium perenne,
Senecio jacobaea,
Urtica dioica.

3.8 Results

Comparability with SCM

Wholly or partially comparable data was collected for eleven of the 16 targets assessed in the SCM (Table 3.7). Data on species composition was mostly comparable or partially comparable. Partial comparability most often occurred because data on the same attribute or species was collected but the scale at which the data was collected was differed from standard SCM protocol, mainly as a result of the limited space in the fenced areas. Measurements of litter and bare ground in the reduced grazing experiment do not differentiate, as the SCM methodology does, between standing dead material and a thatched layer of litter or between disturbed and undisturbed ground.

Height structure

SCM criteria for vegetation height states that a minimum of 25% of the sward should be under 5 cm and minimum 25% over 5 cm. Using the 30 individual height measures made during the July visits, experimental and control plots were compared with this criteria. Measurements of exactly 5 cm did not contribute to either category, but the pattern of change in proportions <5 cm and > 5 cm proportions were not much affected if the 5 cm measures were allowed to contribute to either or both categories.

All the control plots failed the height criteria in July 2011: three sites (numbers 1, 2 and 4) were too short, there were too few measurements at 5cm or more; and three (3, 5 and 6) had too few measurements at 5 cm or less in 2011. One of the 'too tall' sites is very close to the limit and does meet the SCM target in 2012 and 2013; the other control plots fail in all years (See Fig 3.6). All of the fenced plots failed in 2011; 1F 2F and 4F were too short and the others were too tall. By the end of the experiment, reduced grazing had allowed 4F to pass the criteria by increasing the proportion of sward height of at least 5 cm. The proportion of measurements at least 5 cm increased in plot 2F also, from 26%, just enough to pass, to 43% in 2012, 1F comes close to passing in 2013, the proportion of measurement >5 cm has increased to 23.3%. 3F becomes too tall in later years however, and 5F remains too tall (Fig 3.6). Height changes in 6F cause both measurements <5 cm and >5 cm to increase slightly, but the plot continues to fail the criteria.

Reducing grazing improved the fit of some of the shorter greens to the SCM criteria. However, other areas were already classed as too tall at the outset of the experiment or were borderline fit, and reductions in grazing have made these an even poorer fit. Plot 6F was an exception, where shorter patches were maintained in the sward; despite an increase in mean height over the three July periods, the proportion of measurements >5 cm and <5 cm did not change much (Fig 3.6).

Grazing on grasses

The SCM assesses grazing on all live grass shoots and states that this should not exceed 66%. In the reduced grazing experiment, grazing on some individual species was measured. As these were the most common species, it should be fairly representative of the grasses as a whole. Grazing did not exceed 66% on any of *Festuca* Spp., *Poa pratensis* or *Carex* Spp. in July in either fenced or control plots. Reduction in grazing due to fencing was only significant for *Poa* (p=0.034; see Table 3.2, in Chapter 3a).

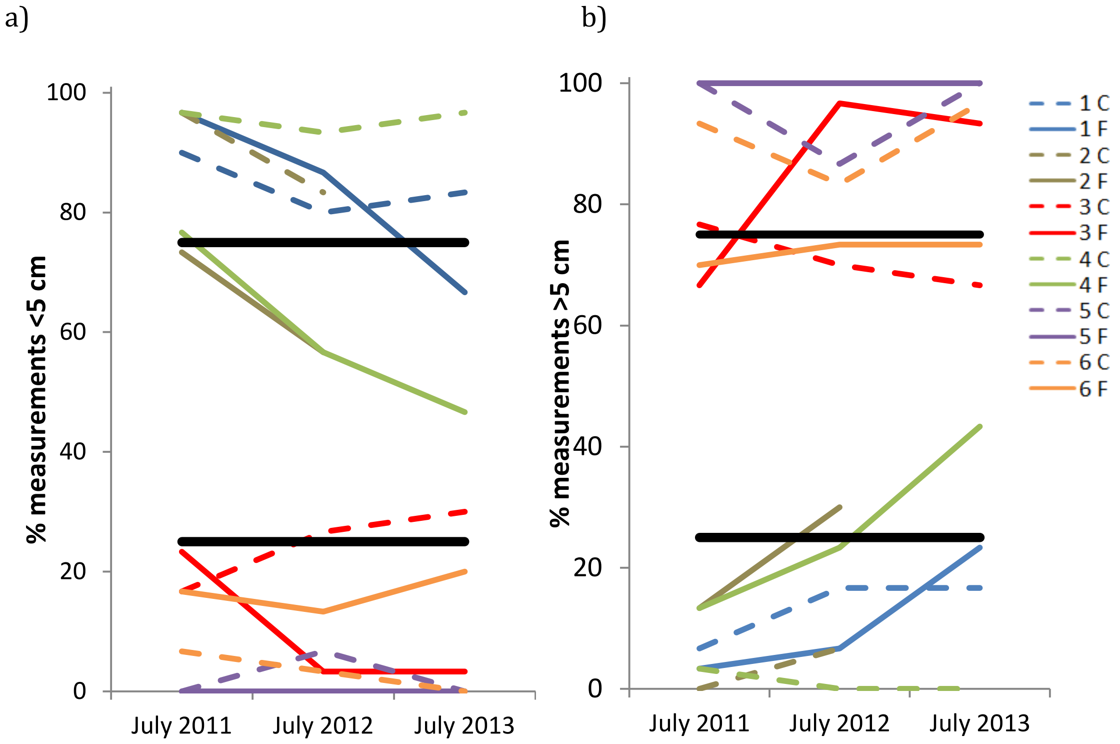

Fig 3.6: proportion of measurements a) <5cm and b) >5cm showing 25% and 75% lines. The area of the graph in which the grassland ‘passes’ the height criteria is between the two horizontal black lines.

Cover of bare ground

Measurements in the fenced plots did not distinguish disturbed bare ground from any other bare ground so measurements could have been an overestimate compared to the SCM criteria. Despite this, bare ground never exceeded the 10% level recommended by the SCM over the four permanent botanical plots within each fenced or control plot. For the July data only, the cover of bare ground was significantly less in fenced plots, but there was no Treatment x Time interaction (p= 0.210) and no interaction with sward height. There was a three-way interaction between Treatment, Time and Starting height when the whole dataset was tested (see Table 3.2), which indicated that bare ground declined in all fenced plots, and declined more in plots that were taller at the beginning of the experiment.

Cover and number of desirable species

All sites had a lower herb cover than the 33% threshold at some point in at least one of the four permanent botanical sub-plots and only two sites (1, 4) ever exceed 33% herb cover when the four sub-plots were averaged (Fig 3.7).

The taller sites (3, 5, 6) had more passes for this threshold outside fenced plots; short sites (1, 2, 4) had more passes inside fenced plots, however this didn't change much over time and therefore cannot be firmly attributed to reduced grazing**.** Herb cover was not related to Treatment x Time interaction (p=0.64), however, there was an interaction between Treatment and Sward height (p= 0.001;Table 3.10) which suggests that plots with initially taller swards lost herb cover after reduction of grazing , whereas the effect was reduced or reversed in initially short plots

Most 1 m x 1 m sub-plots contained at least two indicator species across all years (Table 3.11). Only the tallest site (site 5) had numerous failures to meet this target. At Site 4, one sub-plot failed in July 2011. There was no significant effect of Treatment x Time interaction on the mean number of indicator species present per 1 m x 1 m botanical sub-plot (p=0.80), and no interaction with starting height (p=0.11).

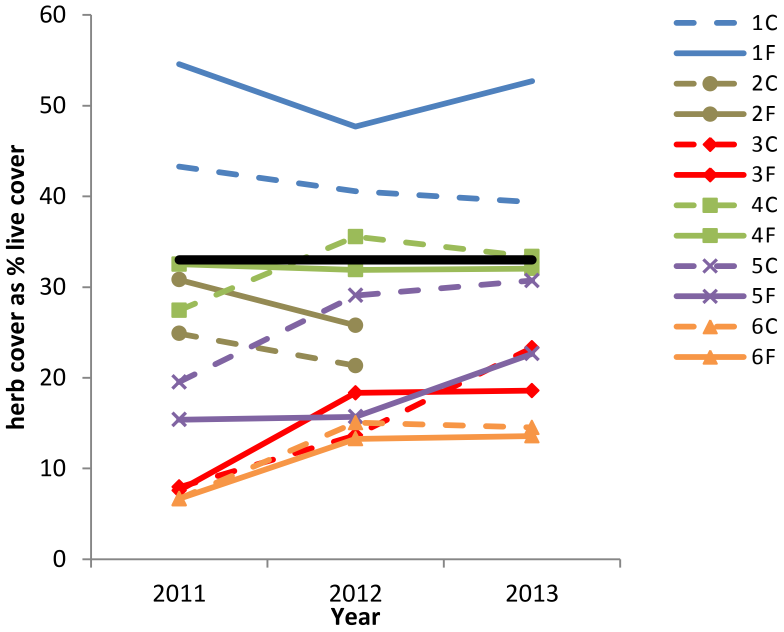

Fig 3.7: Mean herb cover as percentage of live cover for each fenced and control plot in July (mean of four 1 m x 1 m sub plots). The thick black line is 33%, the threshold for passing the SCM.

Cover of undesirable species

In general the cover of undesirable species was very low, and rarely exceeded SCM thresholds. Cover of *Bellis perennis* and *Ranunculus repens* never approached the 25% limit, never totalling more than 2%. No alien species or *Juncus effusus* were recorded. *Arrhenatherum elatius, Cynosurus cristatus* and *Lolium perenne* were the only undesirable species present of those listed in this category of the SCM (Table 3.9) and a few 1m x 1m plots contained 1% or more of these species at times (Table 3.12), but they never exceeded 2% cover. There was no significant relationship between the cover of undesirable species and a Treatment x Time interaction.

Five plots (2C, 2F, 3F, 6C and 6F) had a high cover of (dwarf) shrubs, exceeding the SCM 10% threshold. Sub-plots at two other plots (1F and 3C) exceeded 10% at times. This was mainly due to a high cover of *Calluna vulgaris*. *Erica cinerea* and bracken was present at one site. The cover of shrubs was not significantly altered by the reduction of grazing (p=0.81).

Table 3.10: Results for the effects of Treatment*Time*Starting height (StartHt) models on Log Herb cover as a proportion of live cover, for July data over the three years of the experiment. Other response variables were tested but there were no interactions involving Treatment, so the models are not shown. Response variables with no interactions involving treatment were: Average no. indicator species; % cover undesirable species; % Shrub cover

Response	Significant effects	Coefficient	Std Error	p-value
Log(Herb cover as proportion of live cover)	Intercept	3.42	0.290	
	Time	-0.002	0.008	
	Ht	-0.181	0.070	
	Fence(Vs. Control)	0.427	0.169	
	Time: Ht	0.006	0.002	**0.007**
	Ht: Fence(Vs. Control)	-0.197	0.062	**0.001**

Table 3.11: Number of sub plots (out of four) in each plot that contained two or more indicator species from the list in Table 3.8 Bold type indicates where some plots contained less than two species.

	No. of sub-plots containing 2 or more indicator species (out of 4).			**Mean number of indicator species per sub-plot.**		
Site	**July 2011**	**July 2012**	**July 2013**	**July 2011**	**July 2012**	**July 2013**
1C	4	4	4	3.5	4.5	4.25
1F	4	4	4	4	4.5	4.25
2C	4	4	4	2.5	4.5	NA
2F	4	4	4	4	4.5	NA
3C	4	4	4	2.5	2.75	3.25
3F	4	4	4	3.5	4.25	3
4C	4	4	4	4	3.5	3.25
4F	**3**	4	4	2.5	3	3.5
5C	**2**	**3**	4	2	2	2.5
5F	**2**	**2**	**3**	1.5	1.75	2.25
6C	4	4	4	3.5	4.25	4.75
6F	4	4	4	3.25	4.5	4.5

Table 3.12: Number of sub-plots containing ≥1% cover of undesirable species listed in Table3.9

Site	**July 2011**	**July 2012**	**July 2013**
1C	0	0	1
1F	0	0	0
2C	0	0	NA
2F	0	0	NA
3C	0	0	1
3F	1	0	0
4C	0	1	0
4F	2	0	2
5C	0	1	0
5F	0	0	0
6C	0	0	0
6F	0	1	0

3.9 Discussion

Throughout the experiment most of the control plots would have failed the SCM height criteria in all years, two sites for being too tall and three sites for being too short. Only one control plot fitted the SCM criteria in 2012 and 2013 (but just failed in 2011 for being too tall). Several control plots and sub-plots also failed on one or both of herb cover and shrub cover (plots with *Calluna vulgaris* present). All control plots and subplots passed on cover of bare ground and litter. A few sub-plots failed on cover of undesirable species and on presence of indicator species. Sub-plots failing on indicator species were mainly located at the tallest site (number). A high cover of dwarf shrubs occurred in some areas of grassland; these areas did not fit the target NVC category very well, so the SCM criteria were perhaps not wholly appropriate here.

Reduction of grazing on short plots resulted in a better fit to the SCM height criteria. The reverse was true of the three taller plots; some control plots were already 'too tall', and reducing grazing was expected to make this worse unless some sufficiently heavily grazed patches were maintained in the sward. This may have been the case in site 6 where, despite the mean height decreasing, the proportion of measurements <5 cm did not change much. Reducing grazing on these tall grasslands would make already taller areas more vulnerable to invasion by species such as *Molinia caerulea*, which is widespread and abundant in the Kilmory Glen area and occurs adjacent to the species-rich grassland. Results from Chapter 3a show that the level of browsing on *Calluna vulgaris* continued to be high enough to restrict its growth and spread (minimum browsing was <33% compared to a maximum of 20% recommended for conservation of heather (Pakeman & Nolan 2009). However, heather at a young growth stage or particularly vigorous heather is known to be able to sustain at least 40% grazing without decline (Grant *et al.* 1982), and on this site long term very heavy browsing has kept heather in short, young growth stage, so some spread of heather in areas where grazing has reduced to below 40% may be possible.

The analysis presented in the first part of this Chapter (3a) found that reducing grazing appeared reduced herb cover in taller plots and had little effect or slightly increased cover in shorter plots. The changes to herb cover were not sufficient to make a difference to whether areas of grassland passed or failed SCM criteria for species composition, however. There were no significant interactions with Treatment or Starting height for other indicators related to species composition (number of indicator species, cover of undesirable species). It is likely that the time period was too short, since inception of the experiment, for many changes to species composition to occur. As discussed in the previous half of the chapter, height changes are of sufficient magnitude that they would be expected to cause changes in species composition in the longer term (Hulme *et al.* 1999).

Due to the diversity of the sward, there are a diverse range of responses expected in response to reduced grazing. I have insufficient power to predict long term responses to the change in sward height effected across the range of swards in this experiment. However experiments on U4 *Festuca ovina-Agrostis capillaris-Galium saxatile* grassland community of the National Vegetation Classification (Rodwell 1992) (a more species poor variety of *Agrostis-Festuca* grassland than the grasslands in this study) found that maintenance of the sward at 3.5 or 4.5 cm mean height resulted in a lower cover of competitive grass species (*Molinia caerulea, Deschampsia flexuosa*) and dwarf shrubs compared to sward height of 6 cm, and an increase the cover of *Trifolium repens* (Hulme *et al.* 1999). This suggests that management for high herb cover on this grassland type should aim to maintain sward height at less than 6 cm.

The difference between initial grazing pressures on taller and shorter grassland areas at this site makes it difficult to make management recommendations. Whilst shorter areas would benefit from reduced grazing in terms of fit to recommended sward height and perhaps increased herb cover, reducing grazing would be detrimental to taller areas and to areas that currently fit the height recommendations.

Heterogeneity in the light environment is one means by which grazing increases diversity on grasslands (Hobbs 1996, Cid & Brizuela 1998). Small scale heterogeneity in the light environment at scales of 1-2m in calcareous grassland has been linked to higher species diversity (Gazol *et al.* 2012, Kasari *et al.* 2013). Fine scale heterogeneity is generally increased on lightly grazed compared to heavily grazed pastures (Cid & Brizuela 1998). However, at present there appears to be a bimodal distribution of grazing at the scale of tens to hundreds of metres at the sites, with some areas very heavily grazed, to <5cm summer height, and contrasting taller, lightly grazed areas.

A bimodal distribution of sward heights is commonly reported in agricultural, semi-natural and natural grazed grasslands (e.g. McNaughton 1984, Cid & Brizuela 1998, Olofsson *et al*. 2008, Dumont *et al*. 2012). This results from the preferential grazing of short swards which are more nutrient rich than taller, older growth (Beecham *et al.* 1999)**.** Under this pattern of grazing, when herbivory is reduced, the most heavily grazed area shrinks, without necessarily increasing the intermediately grazed area (Beecham *et al.* 1999, Mouissie *et al.* 2008). Under decreased herbivore numbers, areas with taller swards that are already less fully utilised may become even less grazed as they become less nutrient rich in their later growth stages. In the longer term these areas will perhaps be overtaken by the most competitive species locally present. This scenario would result in a net loss in conservation value of the grassland and therefore any benefit of reductions in grazing to other communities would have to be balanced against this loss.

To meet the height structure criteria, therefore, the evenness of grazing across the grassland area at a scale of tens to hundreds of metres would need to be increased, to increase the area of intermediate grazing where finer scale selection is exercised. As there are many factors that affect the degree and scale of spatial heterogeneity of grazing, it is challenging to work out possible solutions.

There are many other factors in addition to grazing intensity that have been found to affect the degree of fine-scale heterogeneity in grazing and sward height that is generated by large vertebrate herbivores (Adler *et al.* 2001). It can depend on herbivore species: for example, horses are more likely than cattle to generate large grazing patches (Dumont *et al*. 2012, Nolte *et al*. 2014); cattle are less able to select at fine-scales than sheep or deer so would be expected to generate less small scale heterogeneity in height by their direct grazing activities (Gordon & Illius 1988). However, the effects of trampling, urine and dung associated with grazing are also capable of generating spatial heterogeneity in vegetation and will be present under any species of herbivore (Hester *et al.* 2006). The scale of heterogeneity has also been found to depend on the productivity of grassland (Dumont *et al*. 2012) and the vegetation pattern present prior to introduction of grazing or change in grazing regime, which will also be influenced by soil conditions and micro-topography (Adler *et al.* 2001, Scimone *et al.* 2007, Dumont *et al.* 2012)*.*

Cattle grazing might be considered as a means to even out the use of the grassland at a large scale as cattle make more use of taller swards than deer (as they need longer swards to maintain intake) (Illius & Gordon 1987). The use of taller swards by larger herbivores can facilitate grazing by smaller, more selective herbivores that select shorter, more nutrient rich swards resulting from regrowth after grazing by larger herbivores (Hofmann 1989, Arsenault & Owen-Smith 2002). Facilitation of red deer grazing by previous cattle grazing has been demonstrated, so it is possible that this should act to distribute deer grazing impact away from the most heavily grazed swards (Gordon 1988, Kuiters *et al.* 2005). Cattle show a stronger avoidance of dwarf shrubs and dwarf shrub-dominated communities than do deer or sheep, so introducing cattle should only result in minimal increased grazing impacts on heath (Grant *et al.* 1987, Gordon 1989b). Although their introduction could result in increased trampling damage, which mature *Calluna* is very sensitive to (Milne *et al.* 1998, Bokdam 2001). Their willingness to eat tussock forming grasses such as *Nardus stricta* and *Molinia caerulea* would prevent these species from becoming dominant, however, this might reduce small scale heterogeneity in height by reducing the area of tussocks (Grant *et al.* 1996a, Grant *et al.* 1996b), Ponies are already present (at times) in the grasslands in the study site and since they also make more use of high biomass grassland communities, compared to deer, they may already be facilitating use of some of the taller swards. Horses are also more likely to use dead plant material in times of shortage (winter) than either cattle or deer, preventing litter build-up (Gordon 1989c). However, horses are able to make more use of very short swards than cattle, so cattle would perhaps be a better option as they would not exacerbate the grazing on very short swards to the same extent.

In the longer term however, if the introduction of cattle increases the quality of resources available to the deer, the deer population could increase, leading to more intensive grazing again. Increased fecundity has been demonstrated as a result of facilitation in a deer-cattle assemblage in another area of the Isle of Rum, although increased population density as a result was not demonstrated, so the eventual consequences for the population density are uncertain (Gordon 1988). A review of grazing facilitation concluded that there is no evidence of facilitation of grazing of smaller grazers by larger species resulting in population growth of the smaller species, possibly because the benefits of facilitation in the growing season is countered by increased competition for resources outside of the growing season in the presence of the large herbivore, resulting in greater mortality (Arsenault & Owen-Smith 2002). At my study site, there is some evidence that winter mortality in deer at this site is affected by the quality of summer food resources which affects body condition at the start of the winter, so facilitation during the growing season could increase overwinter survival by this means (Clutton-Brock & Albon 1989, Bento 2012). Also red deer utilise heath communities in the winter months, restriction of grassland biomass due to cattle grazing may not be as important as in systems where both the smaller and larger herbivores primarily use grasses (Gordon & Illius 1989, Arsenault & Owen-Smith 2002).

There are potential disadvantages of using larger, less selective herbivores: their lesser ability to select at the bite level scales might decrease small-scale heterogeneity. Introducing cattle could result in increased trampling impacts (Albon *et al.* 2007), increasing the proportion of bare ground. In moderation this can be a positive effect, as trampling creates sites for seedling establishment (Rosenthal *et al.* 2012), but excessive trampling would create large areas of disturbed bare ground, leaving the soil vulnerable to erosion.

Establishing feeding sites or mineral blocks could also spread grazing impacts more evenly. However, these methods create problems of their own, by increasing impact in the immediate vicinity to very high levels (Putman & Staines 2004). Supplementary feeding would also increase the population in the long-term. It may also be considered inappropriate in 'wild' areas.

Suitability of sward height and structure as a metric

Height recommendations are a simple management tool that is easily measurable for any grassland. However, it is not clear how well they translate into benefit for indicator species or species diversity. The shortest plots (from the study here and the areas assessed in the SCM) still contain the minimum number of indicator species despite being 'too short' and the area having been heavily grazed for many years (Pearman *et al.* 2008, Dayton 2011). Unfortunately the time-period of this study was too short to see changes in community composition in response to the height changes. In general, heavier grazing has been found to increase species diversity on these grasslands rather than threaten it (Ball 1974, Virtanen *et al.* 2002). There is little emphasis on larger scale diversity of height or vegetation composition, although the list of indicator species includes both short herbs and grasses and very tall herbs (Table 3.8). These include the tall herbs *Filipendula ulmaria and Angelica sylvestris,* which can reach vegetative heights of >1 m (Kleyer *et al.* 2008). It is not clear that the persistence of these species would be favoured by having 25% of the sward shorter than 5cm at scales of 1m^2. Persistence would likely be dependent on the presence of adjacent taller ungrazed areas and flowering of these species is unlikely at such short sward heights. Furthermore, the prescribed scale of heterogeneity is so small as to be outside of management control and may simply be impossible to achieve on some grasslands. Changes to small scale height heterogeneity following grazing regime change are highly unpredictable (Scimone *et al.* 2007). Choosing grazers that select at fine scales *can* increase small scale heterogeneity, but the outcome is also dependent on underlying species composition and pre-existing heterogeneity of sward structure (Scimone *et al.* 2007, Dumont *et al.* 2012), and so is essentially site specific.

I suggest, based on the above, that the current height standards are too prescriptive. SCM criteria should be altered to take into account the diversity of features that come under the umbrella of 'calcareous grasslands'. In particular, the wider scale structural heterogeneity of the grassland should be taken into account. As part of this, more emphasis should be placed on integrating the requirements of other taxa. Invertebrate taxa often have their highest diversity at taller sward heights than plant diversity, and inclusion of the full range of potential species (including some red list species) is encouraged by inclusion of both tall, ungrazed or rarely grazed and very short swards (Wallis De Vries *et al.* 2002, Dennis 2003, Davies *et al.* 2007). A varied grazing regime would seem to be more compatible with achieving conservation goals in other species groups – many studies of grassland grazing regimes have found that a diversity of grazing levels promotes a wider diversity of invertebrate species (Dennis *et al.* 2002, Dennis 2003, Woodcock *et al.* 2005), and increasing the abundance and diversity of invertebrates has knock on positive effects for the populations of insectivorous bird species (Dennis *et al.* 2002, Dennis 2003, Woodcock *et al.* 2005, Dennis *et al.* 2008).

At a small site of a few ha, there may not be much scope for varying grazing levels without management and rotational grazing of livestock. However, at a larger site like Rum NNR, the variation in grazing levels present across the island, generated by culling and differential habitat use by herbivores will generate variation on various spatial scales. Rather than considering this as a problem for conservation, managers should consider whether maintaining (or allowing), varied grazing levels, including apparently 'undesirable' levels, are in fact likely to benefit other taxa, in which case allowing or encouraging such variation would be justifiable in conservation terms.

Management guidelines for similar habitats in the UK and mainland Europe have also being too prescriptive and encouraging promoting too much homogeneity in the habitats they are designed to promote or preserve. The SCM criteria for lowland calcareous grasslands has previously been criticised for too much focus on plant communities at the expense of other taxa (Davies *et al.* 2007); a problem also identified in the management of similar communities on mainland Europe (Wallis De Vries *et al.* 2002). Management guidelines for calcareous grasslands in mainland Europe have been more generally criticised in a recent review for, not encouraging enough heterogeneity within grassland areas and the surrounding landscape to support the full range of flora and fauna (Diacon-Bolli *et al.* 2012). As discussed above, similar criticism can be levelled at the SCM for upland calcareous grassland (the category that the NATURA habitat species-rich *Nardus* grassland falls into for assessment purposes).

Conclusions

This study highlights that even within a single community type, variation in starting conditions and in grazing intensity can result in difficulties in producing management recommendations. In such a situation, reduction of grazing could benefit some areas of grassland in terms of matching to conservation criteria but would come at cost to other areas. Polarisation of grazing levels within grassland can result in areas of grassland that are not a good fit to conservation sward structure targets. If the spatial pattern of grazing is driven by large-scale grazing lawns, reduction of herbivory may lead to those lawns shrinking, with no net gain to conservation. This would have to be monitored in the event of grazing reduction. However the fact that there is little net change in diversity, species composition or number of species suggests that any adverse changes resulting from short term grazing reduction (a few years) should be fairly easily reversible, in contrast to the difficulty of restoring diversity to grasslands after grazing exclusion, where species may be rapidly lost (see Chapter 2).

Manipulation of the grazing pattern by introducing other species of herbivores is a possible management option; but with the current state of knowledge, the long term consequences of this for grazing patterns and herbivore population dynamics are uncertain.

Lastly, the potential consequences for other plant communities and taxa should be considered. It is likely that following reduction of density, browsing on adjacent heath would be reduced (Oom *et al.* 2010), which would be beneficial to the conservation status of the heath community. Although the polarisation of grazing levels within grassland community may result in grassland missing some conservation goals, there are potential benefits to other taxa of conservation importance of allowing large-scale heterogeneity in grazing levels and sward structure (Dennis 2003, Davies *et al.* 2007, Diacon-Bolli *et al.* 2012).

Chapter 4: Effect of landscape-scale vegetation patterns on grazing impact.

4.1 Summary

- Understanding how the vegetation mosaic influences herbivore behaviour is of great importance to planning conservation management with free-ranging herbivores. I used natural variation in vegetation mosaics on the Isle of Rum, Scotland, to quantify the impact of red deer (*Cervus elaphus)* management on vegetation communities of conservation significance, and how this might be modified by proximity to preferred grassland communities.
- Red deer are the main herbivore on the island. I tested the effects of local deer density and the area of preferentially grazed grassland communities within 250 m, 250-500 m and 500-1000 m on sward height, *Calluna* utilisation and litter depth, between 2001 and 2008, on four communities (Dry Heath, Wet Heath, Alpine Heath and Species-Rich grassland).
- Wet and Dry Heaths, which are less preferred by deer, had lower sward heights where more preferred grassland was present within 1000 m. Unlike previous studies, only a weak relationship was found between *Calluna* utilisation on heaths and preferred grassland within 1000 m.
- The effect of proportion of preferred grassland on the sward height of Species-Rich grassland appeared to be scale dependent. Sward heights were lower on grasslands where the proportion of grassland within 250 m was high. The depth of the litter layer was also negatively correlated with the area of preferred grassland at this scale. However, at larger scales (500 – 1000 m) radius, increased grassland area was correlated with taller swards.
- Deer density had only a slight effect on grazing impacts on the less preferred communities, with some effect on Alpine Heath sward heights.
- On Species-Rich grassland, deer density was positively correlated with *Calluna* utilisation and negatively with inter-tussock sward height.
- The effect of community configuration at the scale of 100s of metres on herbivore grazing patterns should be considered when managing a mix of communities with different grazing requirements. We found that the potential for conflict in

management was increased in areas where the preferred plant community is abundant. Whilst deer densities drove part of the spatial pattern on the preferred community, the patterns of grazing on the less preferred communities are better explained by their position in relation to the preferred community.

4.2 Introduction

The distribution of herbivore grazing and browsing impacts across a landscape is influenced by many factors, including: availability of shelter and water; intra- and inter specific competition; attraction to conspecifics and quality and distribution of food resources (Senft *et al*. 1987, Bailey *et al*. 1996). The spatial distribution of food resources influences patterns of animal behaviour and distribution and consequently influences their patterns of impact on the vegetation (e.g. Clarke *et al*. 1995a, b, Bailey *et al*. 1996, Hester & Baillie 1998, Wallis De Vries *et al*. 1999, Dumont *et al*. 2002, Bee *et al*. 2009, Oom *et al*. 2010).

At small scales the basis for selection is mainly food quality and quantity (Bailey 1996), herbivores generally spend more time in eating higher quality food types and more total time in areas of the landscape with a greater quality and/or quantity of food (Senft *et al*. 1987, Bailey *et al*. 1996). However, the costs of search and travel time (as well as limits in perception) prevent perfect selection of high quality resources (see Bailey *et al*. 1996 for review of mechanisms of selection and see also, Dumont *et al*. 2002, Cromsigt & Olff 2008). Thus the degree of aggregation, arrangement and distribution of preferred and less preferred food or vegetation community types within a landscape can alter the spatial pattern of consumption of both the preferred and less preferred food resource by large herbivores (Clarke *et al*. 1995b, Bailey *et al*. 1996, Cromsigt & Olff 2008).

Dry heath–grassland mosaics, comprising a mixture of patches dominated by *Calluna vulgaris* and by graminoid species have been used as a model system for studying spatial patterns of grazing by ungulates. Compared with most hill-grass species, *Calluna vulgaris* (henceforth shortened to *Calluna*) is both less digestible and less tolerant of grazing (Charles *et al.* 1977, Gordon 1989b). Graminoid-dominated communities are the preferred food resource, when present. An ‘edge effect’ of more intense browsing of heather by sheep and deer at the interface of the dry heath community with preferred grass patches, is well established (Clarke *et al.* 1995b, Hester *et al.* 1996, Oom & Hester 1999). This effect occurs in both summer and winter grazing patterns and extends a few metres into the heath vegetation (Clarke *et al.* 1995b, Hester *et al.* 1996, Hester & Baillie 1998, Dumont *et* *al.* 2002, Palmer *et al.* 2003, Oom *et al.* 2010). Fewer studies have considered the influence of resource configuration on the spatial pattern of utilisation of the preferred resource in this mosaic, (but see Hester & Baillie 1998) so little is known about how associated, grazing-tolerant vegetation communities (grassland) are affected. Elevated use of less preferred resource in close proximity to a preferred one has been found in other systems at similar scales (metres to hectares in size) (Clarke *et al*. 1995b, Hester *et al*. 1996, Oom & Hester 1999, Dumont *et al*. 2002). Conversely, in areas of mainly low quality resources, the preferred resource is sometimes less used (Barbosa *et al.* 2009, Bee *et al.* 2009).

Few studies have looked at the effect of community patterns at larger scales, (100s of metres or more). The spatial scale considered is important as small-scale patterns of selection do not always scale up to larger areas, as different constraints and selective mechanisms come into play as the spatial (and implicitly, temporal) scales are increased (Bailey *et al.* 1996, Mayor *et al.* 2009). It might be expected that as other factors become limiting, food quality becomes a less important influence on herbivore grazing pattern. However, those studies that have addressed the effect of a proportion of high quality resource in the landscape did find elevated use of resources in areas with more high quality food (Palmer *et al.* 2003, Speed *et al.* 2009). This increased use of resources in proximity to a preferred food type is similar to the well documented increased utilisation of plant communities in proximity to waterholes on arid rangeland (Jeltsch *et al.* 1997) , and in the vicinity of supplementary feeding sites in temperate forest (van Beest *et al.* 2010a, Mathisen *et al.* 2014), both of which extend over 100s m to several kilometres (Mathisen *et al.* 2014).

This is relevant to rangeland management, especially where free-ranging (usually wild) herbivores are involved, as there is less control over their movements compared with managed domestic stock. Where vegetation communities that require different levels of grazing to meet management aims exist side by side, there will be a trade-off in managing for the condition of one community over another, unless the combination of herbivore preference and the accessibility and tolerance to grazing of the vegetation communities create a favourable distribution of impact. Little is known about the importance of the community mosaic to patterns of use on naturally occurring mosaics of open habitats other than the model dry heath-grassland system, yet there are extensive areas of other types of communities in the temperate zones that both are grazed and of conservation interest (e.g. Halada *et al.* 2011).

The goal of this study was to increase the understanding of how small-scale herbivore impacts on both preferred and less preferred communities in a complex mosaic are influenced by local deer density and the surrounding vegetation at a scale of hundreds of m to km.

It is expected that higher impact will be found on all communities where there is a higher proportion of the preferred community. It is also expected that higher impacts on all communities should be found at higher local (a few km^2) deer density.

4.3 Methods

Study site

The Isle of Rum is an island (107 km^2) located 25 km off the west coast of Scotland (57^0 00'N, 6^0 22' W). The climate is oceanic, an average annual rainfall of 2500 mm is recorded at sea level in the east of the island (Clutton-Brock *et al.* 1982). The study area encompasses the entire island outside of the deer fenced area (see Fig 4.1). The terrain is rough and mountainous (the highest point is the summit of Askival at 812 m) and, away from main valleys and ridges, largely pathless, making access to some areas difficult. The main vegetation types are wet heath and blanket bog; smaller areas of dry and herb rich heaths are also present (Pearman *et al.* 2008). Areas of both acid and calcareous *Agrostis-Festuca* grassland are present on the coast and in upland areas (Fig 4.2) (Bates *et al.* 2002; Pearman *et al.* 2008), and these are preferentially grazed (Charles *et al.* 1977, Gordon 1989b).

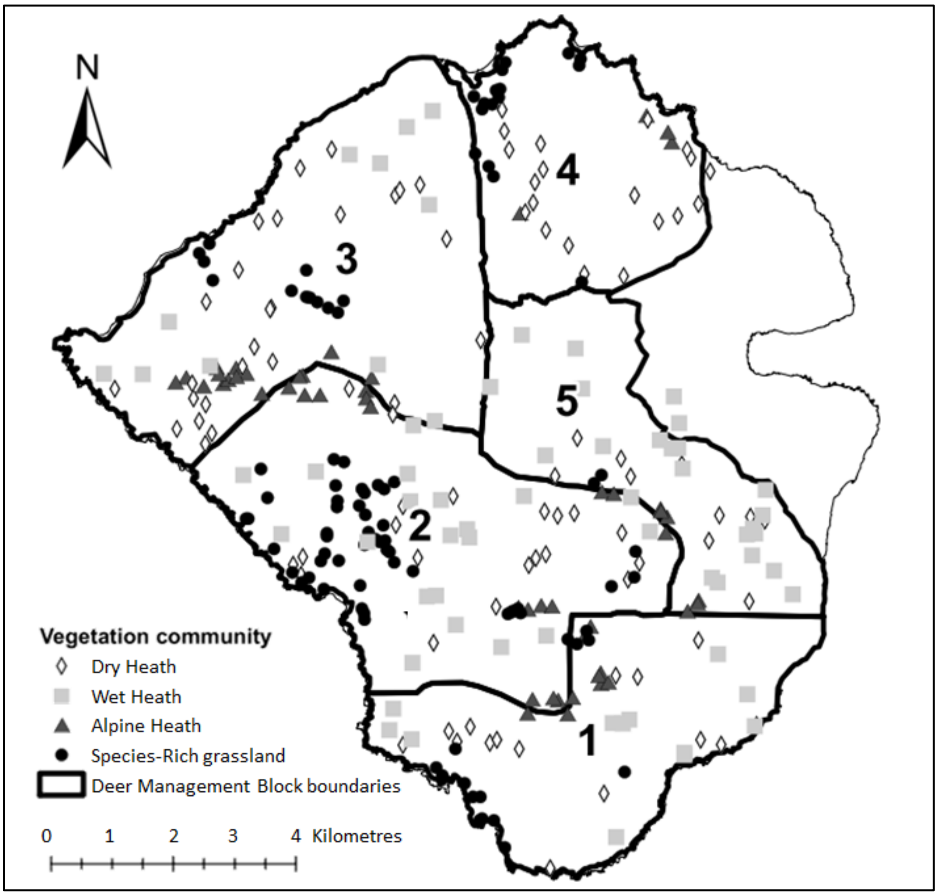

Fig 4.1: Map of Rum, showing boundaries of deer management blocks (DMB) and plot locations. The unlabelled area is surrounded by a deer fence and is not routinely counted. A few survey plots were located within this area, these are not included in the analysis.

A NATURA habitat monitoring exercise commissioned by Scottish Natural Heritage (SNH) and carried out by the James Hutton Institute (JHI, formerly the Macaulay Land Use Research Institute), between 2001 and 2008 (Britton & Pakeman 2009) provided an opportunity to test the hypotheses posed. Red deer (*Cervus elaphus*) are the main herbivore on the island, which is divided into five deer management blocks (DMB) (Fig 4.1). Deer densities differ widely between blocks (see Fig 4.3 and Table V.1 in Appendix V) partly as a result of differential culling in the period 1991-2000 (Clutton-Brock *et al.* 2002a). Block boundaries do not represent a physical boundary or fence, however hind home ranges on Rum are small (averaging 200-400 ha) compared to block areas, and hinds generally remain hefted to their home range throughout their lives (Lowe *et al.* 1966). A differential culling experiment found that it was relatively easy to reduce hind numbers in a DMB, without causing an influx from other areas; stags are more mobile, shifting range seasonally during the rut, and more stags migrated between blocks when densities were altered by culling (Clutton-Brock *et al.* 2002a). The annual island-wide cull target is usually broken down into separate targets for blocks 1, 2, 3, and 5, whilst DMB 4 has not been culled since 1972 (Pearman *et al.* 2008). Other large herbivores present on the island are approximately 40 cattle, which spend most of their time in DMB 2, and around 20 ponies, which divide their time between DMB 2 and DMB 4. Feral goats are also present (mainly in DMB 1, 2 and 3); precise goat numbers at the time of the study are unknown but were thought to be approximately 200 - 300.

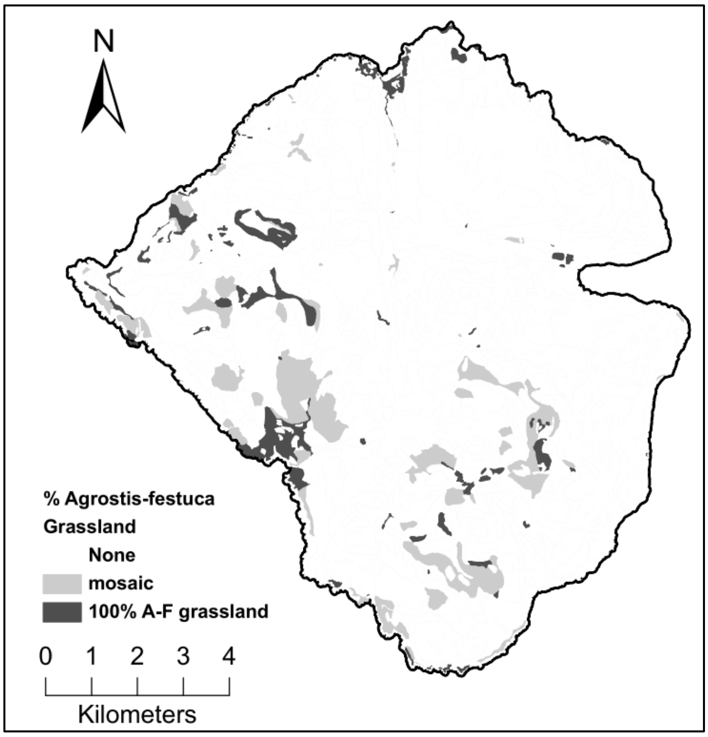

Fig 4.2: The locations of *Agrostis-Festuca* grassland on Rum, based on a 1998 survey by Bates *et al*. (2002). Some areas in this survey were defined as 'mosaics' of more than one community type, such areas are shown where they include *Agrostis-Festuca* grassland.

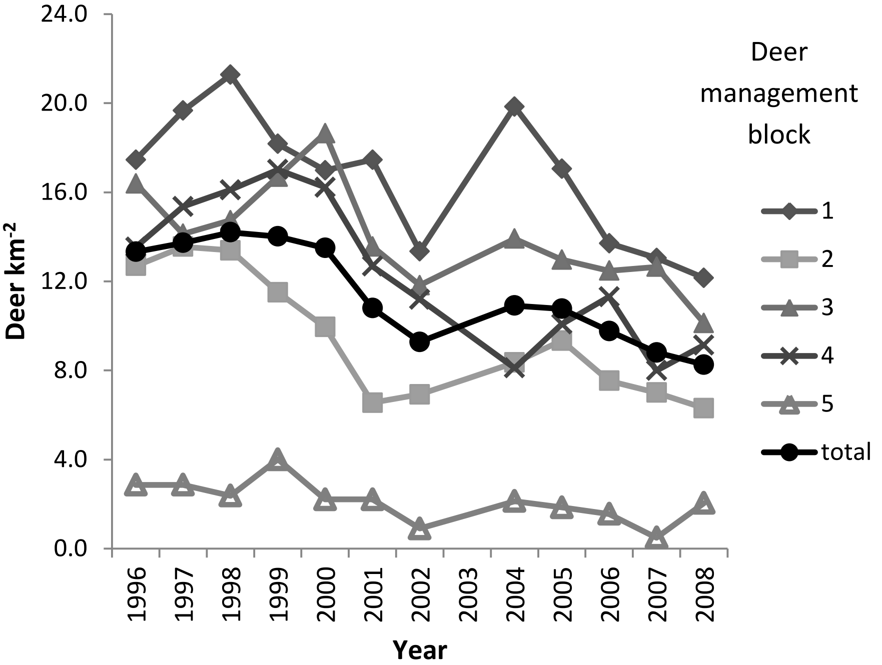

Fig 4.3: Deer density calculated from DCS annual count 1996-2008, divided into blocks. There was no count in 2003.

Fieldwork methodology

In 2001/2, three hundred vegetation monitoring plots were established in four NATURA communities protected under Annex 1 of the Habitats directive (Council of the European Communities 1992): Northern Atlantic wet heaths with *Erica tetralix* (Wet Heath), European dry heaths (Dry Heath), Alpine and boreal heath (Alpine Heath) and Species-rich *Nardus* grasslands on siliceous substrates in mountain areas (henceforth referred to as Species-Rich Grassland (SRG)). Communities are referred to hereafter using the short names in parentheses. The number of plots was split between communities according to areal extent and plots were established in randomly determined locations in each community type (Table 4.1; Fig 4.1; Table VI.1).

The definition of Species-Rich *Nardus* Grassland encompasses several National Vegetation Classification (NVC) community types dominated by *Agrostis-Festuca* species, namely: CG10 (*Festuca-Agrostis-Thymus* grassland) and CG11 (*Festuca-Agrostis-Alchemilla* grass-heath) (and all sub-types of these communities); also the more species-rich types of U4 (species poor, acid *Festuca-Agrostis-Galium* grassland). Species-rich varieties of *Nardus stricta*-dominated U5 (*Nardus stricta – Galium saxatile* grassland) are also included (JNCC, 2012) (NVC names and descriptions from Rodwell, 1992). These grasslands are more tolerant of heavy grazing than heath-dominated communities, but *Agrostis-Festuca-*

dominated grasslands are vulnerable to species loss if grazing levels are low (Ball 1974, Rawes 1981, MacDonald *et al.* 1998a).

Table 4.1: Number of plots within each vegetation community established and re-visited in each year of recording

Vegetation Community	Plots established 2001/2	Re-recorded 2003	Re-recorded 2007	Re-recorded 2008
Species-rich Grassland	94	84	--	86
Alpine Heath	50	44	--	45
Dry Heath	91	69	86	--
Wet Heath	65	55	62	--

In August/September 2001 and 2002 the plots were marked, with a wooden post and two metal pegs inserted flush with the ground, and vegetation data were collected. In August/September of 2003 all plots that could be relocated were re-recorded. In October 2007 plots on Wet and Dry Heath were re-recorded and in July/August 2008 Species- rich grassland and Alpine Heath plots were re-recorded (see Table 1). GPS and the plot markers were used to precisely relocate plots. Where the post was lost, photos, sketch maps, and a metal detector were used to aid relocation. Plot losses occurred due to loss of markers on plots lacking other features to relocate them. Poor weather conditions, particularly in 2003, meant some plots could not be safely accessed within the time available.

Twenty measurements of sward height were made at 1 m intervals on two 10 m transects within the plots. On Alpine Heath and Species-Rich grassland, where distinct tussocks were present, measurements of tussock and inter-tussock height were made separately. Sward height data was collected on all three visits on all vegetation communities. There were insufficient tussock height measurements made on Alpine Heath to include in the analysis. On Species-Rich grassland, in 2008 only, the depth of the litter layer was recorded to the nearest cm at the same points. No measurable litter layer was observed in previous years.

One shoot of *Calluna vulgaris* at each point (where present) was scored on a four point scale following the method of Grant *et al.* (1981): 0 – ungrazed, 1 - <50% current year long shoot removed, 2 - >50% current year long shoot removed, 3 – 100% current year long shoot removed plus some of the previous year's growth. The mean value for sward height, and litter depth was calculated for each plot, and these are the values used as response variables in this study. For *Calluna* the average proportion of current year's growth removed was calculated using the following equation, following the method of Hester & Baillie (1998) (U0, 1, 2, 3=number of plots in each utilisation category):

$$\%\ \text{utilization} = (0.3(U1) + 0.8(U2) + 1.2(U3))/\ 100(U0 + U1 + U2 + U3) \qquad \text{eqn 1}$$

Calluna utilisation was collected on all visits to Alpine heath plots, and in 2001 and 2007 on Wet and Dry heaths, and in 2003 and 2008 on Species-Rich grassland. *Calluna* utilisation is a direct measure of grazing pressure, used to assess herbivore impact on heather-dominated communities. Sward height and litter depth, representing the balance of vegetation growth and herbivory, are indicators of herbivore impact on grass-dominated communities (MacDonald *et al.* 1998). Where the sward contains long-lived and relatively slow growing dwarf shrubs, sward height will reflect a combination of past and present years' conditions, particularly under a trend of declining grazing.

The three Alpine Heath plots in DMB 4 were removed from the analysis as they are at low altitudes (<100 m), therefore not meeting the criteria for definition as Alpine Heath, and substantially lower than all other Alpine Heath plots (294 to 754 m) (see Table V.3).

Explanatory variables

For all plots topographical exposure was scored by summing the angle to the horizon at the eight major compass points (TOPEX score) (Pyatt 1977). The Ordnance Survey digital terrain model of the island was used to calculate the elevation of each survey point.

A digitised vegetation map produced by a 1998 survey (Bates *et al.* 2002), classifying all communities by NVC types, was used to identify areas of preferentially grazed *Agrostis-Festuca* grasslands (Fig 4.2). *Agrostis-Festuca* grassland was defined to include areas identified as: U4, CG10, CG11 (Rodwell 1992) and all sub-types of those communities. This definition overlaps broadly with the JNCC definition of species–rich *Nardus* grasslands (see above). U5 was not included in the 'preferred grasslands' as it was thought that communities dominated by *Nardus* were not the most preferred resources. Vegetation communities recorded as mosaics of more than one NVC class were assigned a value according to the proportion of '*Agrostis-Festuca* grassland' NVC type(s) present. If this was not recorded during the 1998 survey, it was assumed that the area contained equal proportions of each type listed. Percentage *Agrostis-Festuca* grassland within three zones formed by concentric rings of 0 – 250 m, 250 – 500 m and 500 – 1000 m from the plot centre was calculated. These concentric rings rather than the total areas within them were used in order to reduce correlation between the variables. The minimum distance that could be considered was restricted by data resolution. The maximum distance considered (circle of area 314 ha) is comparable to the average home range size of hinds on Rum (see above).

Deer numbers were obtained from the annual Deer Commission for Scotland (DCS) deer count, available at the level of deer management block (DMB). The counts were carried out in spring (Feb-Mar), by helicopter in 2004-2008, prior to that, by counts on the ground. Previous years' calves were excluded as only numbers of animals over one year old could be obtained to block level prior to 2002. Hind: calf ratios were not significantly different between blocks for the years 1981-2001 (Clutton-Brock *et al.* 2002a), so their exclusion should not affect the comparative densities greatly. Counts could not be found for DMB 4 before 2002, in these years the DMB 4 numbers were calculated from the spring (Jan – May) ground-based censuses carried out as part of the individual-based Red Deer Research Project based in this area. In the years where comparable data is available (when the DCS count was ground based) this count found on average 7% more deer than the DCS count. The area of each deer block and the area of *Agrostis-Festuca* grassland (calculated in ArcGIS 9), were used to calculate deer density km^{-2} and deer km^{-2} of grassland in each block for each year of the survey (see Fig 4.3; Table 4.2). The overall island deer count in 2008 was 23.5% lower than in 2001 (Table V.1 in Appendix V).

Table 4.2: Total area of *Agrostis-Festuca* grassland and 2001 deer density for each DMB.

	DMB 1	DMB 2	DMB 3	DMB 4	DMB 5	TOTAL
Agrostis-Festuca grassland (km^2)	0.93	2.14	1.53	0.43	0.43	5.46
Total area (km^2)	16.8	24.4	23	17.5	12.2	93.9
% area which is *Agrostis-Festuca grassland*	5.54	8.76	6.65	2.46	3.52	5.81
Deer density in 2001	17.5	6.6	13.6	17.8	2.2	11.7
Deer per km^2 *Agrostis-Festuca grassland in 2001*	317	74.8	204	721	62.5	202

Statistical analysis

All statistical analyses were carried out in R, version 2.15 (R Core Team 2013).

Linear mixed models

Linear mixed models were used to analyse the data, using plot ID as a random term to account for repeated measures. The package nlme (Pinheiro *et al.*) was used to run linear mixed models. An approximation of the variance explained by the mixed models was calculated following the method of (Liu *et al.* 2008) for fixed effects (R^2_F) and the full model (R^2_T). I used the commonality analysis as described by (Seibold & McPhee 1979) to calculate the proportion of the total variance explained by each fixed effect (unique effects), and to the combined effect of two or more (common effects) are calculated.

I tested whether utilisation measures were associated with: micro-climate (Elevation and TOPEX); the percentage *Agrostis-Festuca* grassland within three concentric rings (as described in section 2.2.2); and deer management block (DMB - as a categorical explanatory variable), as in addition to differences in deer density, the DMBs differ in: the presence of other herbivore species in some blocks (see section 2.1); climate, especially rainfall; and in terrain. I also included year in the model as a categorical variable, in addition to deer density changes, inter-annual differences in plant growth will affect sward height and might affect *Calluna* utilisation indirectly. The full model was thus:

$$y \sim Yr + DMB + E + T + G1000 + G500 + G250 + \varepsilon \qquad \text{eqn 2}$$

Where y was the response variable (either sward height or *Calluna* utilisation); Yr =effect of year (as a categorical variable); E=elevation; T=TOPEX; G1000, G500, G250 were the effects of the percentage *Agrostis*-*Festuca* grassland present within the three concentric rings; and ε=random effects. From the full model, stepwise model simplification was carried out under ML estimation (based on likelihood ratio F-tests by ANOVA) and the final model tested for goodness of fit through analysing residuals plots. Data transformation was carried out as necessary to remove trends in residuals.

To investigate the role of deer density, the analysis was repeated with one of four measures of deer density (model 3 a-d below). DMB and deer density are highly correlated, so DMB was included in models from the equation 3 group only if it fitted in addition to deer density. Year was removed, as it was confounded with deer density:

$$y \sim DMB + E + T + DDCY + G1000 + G500 + G250 + \varepsilon \qquad \text{eqn 3a}$$

$$y \sim DMB + E + T + DD5CY + G1000 + G500 + G250 + \varepsilon \qquad \text{eqn 3b}$$

$$y \sim DMB + E + T + DGCY + G1000 + G500 + G250 + \varepsilon \qquad \text{eqn 3c}$$

$$y \sim DMB+ E + T\ DG5CY + G1000 + G500 + G250 + \varepsilon \qquad \text{eqn 3d}$$

The deer density measures were deer density (DDCY) and deer per km^2 of *Agrostis*-*Festuca* grassland (DGCY) in the same year as the response variable was recorded. For sward height and Litter depth, (but not *Calluna* utilisation, as it represents utilisation only in the current year) also the 5-year mean (up to contemporary year) deer density (DD5CY) and deer per km^2 *Agrostis*-*Festuca* grassland (DG5CY). Only the best-fitting model (based on AIC score) from the equation 3 group is reported; where this differs from the final model resulting from equation 2, both models are reported.

Spatial autocorrelation (SAC) was found in some model residuals (see Appendix VI for methods). Fitting DMB as a second random effect (models fitted using 'lmer' in the package lme4 (Bates *et al.* 2014) removed SAC in some models, and p-values were calculated by likelihood ratio tests via ANOVA. As a second approach, all interactions between year or deer density and other significant fixed effects were considered (for all models whether there was SAC in residuals or not) and significant interactions retained where they improve explanatory power (adjusted R^2_F). Fitting these interaction terms was successful in removing SAC in four of six cases where SAC had occurred in the residuals of only some years of the data.

Linear models

Linear modelling was used to analyse the litter depth data for 2008. The model was fitted using the generalised least squares function in the package nlme to allow a spatial correlation term to be fitted to account for SAC in the residuals. The same fixed effects as above were included in the starting model, except that deer density measures were from the previous year and mean of five years up to the previous year, as litter depth will reflect grazing pressure in the previous year or several years. Stepwise model simplification was carried out (based on p-values), and the final model tested for goodness of fit through analysis of residuals plots. Variance partitioning was used to assess the contribution of each fixed effect to the total model R^2 (Mood 1969).

4.4 Results

Sward heights

Explanatory power of models

Fixed effects accounted for >60% of the variance on Alpine Heath and between 20-30% (adjusted R^2_F) of the variation on other communities (Table 4.3a, b). Models with deer density (and sometimes DMB) included were able to explain a similar level of variation to models with year (and sometimes DMB) included, except for tussock height on Species-rich Grassland (SRG), where interactions with year where important. There was unresolved spatial autocorrelation in the Alpine Heath model and the inter-tussock height model on Species-rich Grassland including deer density, which could have biased the model coefficients. There were no other trends in the residuals.

Wet heath

On Wet heath, sward height was higher in 2003 than in 2001/2. No interactions between year and other model terms were found. The negative correlation between elevation and sward height (Table 4.3a) suggests climatic restriction on sward height. Sward height was lower where there was more *Agrostis-Festuca* grassland within the vicinity (G250; Table 4.3a), G250 accounts for 6.8% variance in the model including year and 4.4% in the model with deer density. In the alternative modelling incorporating deer density, DG5CY was significant but accounted for just 0.9% of variance (Table 4.3b).

Dry heath

On Dry heath, sward height was higher in 2007 than in 2001/2. No interactions between year and other model terms were found. The negative correlation between elevation and sward height again suggests climatic restriction on sward height (Table 4.3a). Sward height was lower where there was more G1000 (Table 4.3a), *Agrostis-Festuca* grassland accounted for 15.9% of variance in the data in the model including year, 5.8% when DD5CY was included. DD5CY shows a statistically significant but very small (accounting for R^2_F of 0.9%) positive correlation with sward height (Table 4.3b).

Alpine Heath

On Alpine heath, sward height was higher in both 2003 and 2008 than in 2001/2. No interactions between year and other model terms were found. The negative correlation between elevation and sward height again suggests climatic restriction on sward height (Table 4.3a). Taller swards were found where there was more G1000 (r^2 = 9.0%; 5.8% in Year model, Deer density model, respectively). Sward height was negatively associated with DD5CY, which accounted for 3.2% of variance (Table 4.3b).

Table 4.3a: Best fitting models for sward height, with year and DMB included in starting model. p-values calculated by likelihood ratio tests via ANOVA. The variance solely attributable to each fixed effect is shown in the final column (r^2).

Community	Response	Random effect parameters	R^2_F/ adjusted R_{2F}	R^2_T	Significant fixed effects	Coefficient	S.E.	p-value	r^2
Wet heath	Mean height	plotID	0.302/ 0.277	0.855	Intercept	27.5	1.93		
					Year 2002 (vs.2001)	0.791	1.476	0.593	
					Year 2003 (vs.2001)	2.42	0.686	<0.001	**1.0%**
					Year 2007 (vs.2001)	1.18	0.662	0.078	
					Elevation	-0.033	0.008	<0.001	**17.0%**
					G250	-0.446	0.163	0.008	**6.8%**
Dry Heath	Mean Height	plotID	0.292/ 0.268	0.918	Intercept	24.7	2.34		
					Year 2002 (vs.2001)	-0.706	1.19		
					Year 2003 (vs.2001)	1.357	0.633	0.029	**-1.8%**
					Year 2007 (vs.2001)	1.22	0.59		
					Elevation	-0.02	0.008	0.009	**5.9%**
					G1000	-0.735	0.185	<0.001	**15.9%**
Alpine Heath	log(mean height)	plotID	0.666/ 0.634	0.902	Intercept	3.07	0.473		
					Year 2002 (vs.2001)	0.220	0.100		
					Year 2003 (vs.2001)	0.355	0.09	<0.001	**5.0%**
					Year 2008 (vs.2001)	0.406	0.085		
					DMB 2 (vs. DMB 1)	-0.143	0.181	0.435	
					DMB 3 (vs. DMB 1)	0.138	0.216	0.526	**13.1%**
					DMB 5 (vs. DMB 1)	-0.669	0.215	0.004	
					Elevation	-0.004	0.001	<0.001	**17.3%**
					G1000	0.058	0.017	0.001	**9.0%**
Species-Rich Grassland	log(inter-tussock height)	plotID	0.295/ 0.254	0.832	Intercept	1.61	0.144		
					Year 2002 (vs. 2001)	-0.580	0.367	0.117	**7.2%**
					Year 2003 (vs. 2001)	0.244	0.073	0.001	
					Year 2008 (vs. 2001)	0.469	0.070	<0.001	
					DMB 2 (vs. DMB 1)	0.141	0.161	0.386	
					DMB 3 (vs. DMB 1)	0.649	0.189	<0.001	**10.0%**
					DMB 4 (vs. DMB 1)	0.086	0.168	0.607	
					DMB 5 (vs. DMB 1)	0.002	0.332	0.995	
					G1000	0.024	0.008	0.005	**9.2%**
					G250	-0.007	0.003	0.017	**2.7%**
					Year 2002: G1000	0.112	0.079	0.161	
					Year 2003: G1000	0.009	0.005	0.073	**0.4%**
					Year 2008: G1000	-0.014	0.005	0.005	
	Tussock mean height	plotID	0.231/ 0.199	0.726	Intercept	17.0	1.75		
					Year 2002 (vs. 2001)	8.05	18.9	0.671	
					Year 2003 (vs. 2001)	2.31	1.70	0.177	**11.5%**
					Year 2008 (vs. 2001)	9.72	1.66	<0.001	
					G1000	0.425	0.119	<0.001	**4.3%**
					G250	-0.121	0.045	0.007	**5.2%**
					Year 2002: G1000	-3.79	4.60	0.412	
					Year 2003: G1000	-0.128	0.137	0.349	**2.5%**
					Year 2008: G1000	-0.411	0.124	0.001	

Species-Rich *Nardus* grassland

On Species-rich Grassland, both tussock and inter-tussock sward height were taller in 2003 and 2008 than in 2001/2 (Table 4.3a). There was no correlation between elevation and inter-tussock height, indicating that other constraints (such as grazing) were more important for determining inter-tussock height on this community, even though *Species-Rich* grassland has an altitudinal range similar to the Wet and Dry heaths (see Table V.1). Tussock height is related to elevation, but the correlation does

Inter-tussock mean height was associated with percentage *Agrostis-Festuca* grassland (Table 4.3a). The relationship appears to be complex; it was positively correlated with G1000, but negatively correlated with G250 (Table 4.3a). The contribution to explained variance was greater for G1000 (9.2, 7.3%) than G250 (2.7; 4.2%), in both models (Table 4.3a, b). There was an interaction between G1000 and year (Table 4.3a), but this was of negligible explanatory power. DMB 3 plots had significantly taller inter-tussock height than other areas, after deer density was accounted for. Deer km^{-2} grassland (mean value over 5 years) was significantly correlated with inter-tussock sward height (6.3% variance).

Deer density was correlated with tussock sward height but only explained 0.9% variance.

The relationships between tussock height and the proportion of grassland were in the same direction as on inter-tussock height. However, the effect of G250 appears to be more important, explaining 5.2-4.2% of the variance, whilst G1000 is only significant in the model including year (Table 4.3a, b). There is an interaction between year and G1000, accounting for a further 2.5% variance, the effect of G1000 is reduced to near zero in 2008. With year excluded, the model fixed effects explained only a very small proportion of the variance (Table 4.3b). DD5CY is negatively correlated with tussock height, but the explained variance is very small (0.9%). Interaction effects including deer density were considered; in some cases these were statistically significant, but were uninterpretable, as they predicted increased sward height where there were more deer, in some cases.

Litter layer

Species-Rich grassland litter layer depth was negatively related to G250. The litter layer found in DMB 3 was significantly deeper compared with DMB 1, 4 and 5 (Table 4.4), this was not due to differences in deer density between blocks. Spatial autocorrelation in the model residuals was accounted for by adding a spatial correlation structure.

Table 4.3b: Best fitting models for sward height, deer density included in starting model, year excluded. DMB included only where significant in addition to deer density. The variance solely attributable to each fixed effect is shown in the final column (r^2).

Community	Response	Random effect parameters	R^2_F/ adjusted R_{2F}	R^2	Significant fixed effects	Coefficient	S.E.	p-value	r^2
Wet Heath	Mean height	plotID	0.300/ 0.279	0.855	Intercept	30.7	1.95		
					DG5CY	-0.011	0.003	<0.001	**0.9%**
					Elevation	-0.036	0.008	<0.001	**0.9%**
					G250	-0.395	0.163	0.019	**4.4%**
Dry Heath	Mean height	plotID	0.309/ 0.295	0.681	Intercept	22.5	2.80		
					DDCY	0.345	0.168	0.041	**0.9%**
					Elevation	-0.020	0.008	0.009	**8.6%**
					G1000	-0.836	0.178	<0.001	**5.8%**
Alpine Heath	log(mean height)	plotID	0.642/ 0.616	0.907	Intercept	5.22	0.667		
					DD5CY	-0.111	0.027	<0.001	**3.2%**
					Elevation	-0.004	0.001	<0.001	**16.9%**
					DMB 2 (vs. DMB 1)	-1.03	0.283	<0.001	**16.5%**
					DMB 3 (vs. DMB 1)	-0.132	0.228	0.567	
					DMB 5 (vs. DMB 1)	-2.32	0.458	<0.001	
					G1000	0.057	0.016	0.001	**5.8%**
Species-Rich grassland	log(inter-tussock mean)	plotID	0.226/ 0.194	0.736	Intercept	1.92	0.174		
					DG5CY	-<0.001	0.001	0.952	**6.3%**
					DMB 2 (vs. DMB 1)	-0.025	0.168	0.882	**22.3%**
					DMB 3 (vs. DMB 1)	0.773	0.192	<0.001	
					DMB 4 (vs. DMB 1)	0.365	0.194	0.063	
					DMB 5 (vs. DMB 1)	-0.122	0.336	0.717	
					G1000	0.062	0.013	<0.001	**7.3%**
					G250	-0.007	0.003	0.012	**4.2%**
	Tussock height	plotID	0.049/ 0.022	0.659	Intercept	34.4	3.28		
					DD5CY	-0.818	0.203	0.0001	**0.9%**
					Elevation	-0.013	0.006	0.033	**2.8%**
					G250	-0.108	0.050	0.030	**4.2%**

Table 4.4: Litter depth on Species-Rich grassland. Model with correlation structure fitted. The variance solely attributable to each fixed effect is shown in the final column (r^2).

Response	Correlation structure	R^2_F/ adjusted R^2_F	Significant fixed effects	Coefficient	S.E.	p-value	r^2
Litter depth (cm)	Exponential spatial correlation range 156.35	0.185/ 0.097	Intercept	1.43	0.499	0.005	
			G250	-0.02	0.008	0.019	**10.8%**
			DMB2 (vs. DMB 1)	0.308	0.526	0.560	
			DMB 3 (vs. DMB 1)	1.57	0.682	0.024	**8.4%**
			DMB 4 (vs. DMB 1)	0.141	0.630	0.824	
			DMB 5 (vs. DMB 1)	-0.74	1.11	0.507	

Calluna utilisation

Explanatory power of models

Models fixed effects accounted for a similar level of utilisation as in the sward height models ~20-30% (Table 4.5a, b). No spatial autocorrelation was present in *Calluna* model residuals.

Wet Heath

None of the tested variables explained *Calluna* utilisation on Wet Heath.

Dry Heath

Difference between years was the most important factor contributing to variation in *Calluna* utilisation. *Calluna* utilisation was significantly lower in 2007 than in 2001/2, accounting for 12.5% variance. There was an interaction between G1000 and year, accounting for most of the additional variation in the model. Utilisation was higher where there was a high proportion of grassland 500-1000 m away in 2001, but this effect was smaller in 2002, and non-existent In 2008, where very little utilisation was recorded overall (Table 4.5a).

DG5CY was significantly and positively correlated with *Calluna* utilisation but this did not account for all the difference between years, only accounted for 3.9% of the variance in the data (Table 4.5b). The main effect of Elevation explains 3.2% variation when year is not included in the model. There is also an interaction between elevation and year, with elevation having no effect on 2008.

Alpine Heath

Calluna utilisation was significantly lower in 2007/8 than in 2001/2. Utilisation was highest in DMB 1; the differences in utilisation between DMBs were unrelated to deer density (Table 4.5a).

Species-Rich Grassland

Calluna utilisation was significantly lower in 2008 compared with 2003. Year interacted with DMB, mainly due to DMB 3, where utilisation of *Calluna* was highest in 2003, but lowest in 2008 (Table 4.5a). *Calluna* utilisation was also positively correlated with G1000, but this explained only 1.8% variance (Table 4.5a). In the deer density model, *Calluna* utilisation was positively correlated with DGCY, accounting for 6.8% of the variance, but there was still an additional effect of deer block (Table 4.5b). With deer km^{-2} grassland included, there is a positive correlation with the area of grassland within 250-500 m, accounting for 3.7% of the variance

Table 4.5a: Best fitting models for *Calluna* utilisation (year and DMB in full model). The variance solely attributable to each fixed effect is shown in the final column (r^2).

Community	Response	Random effect	R^2_F/ adjusted R^2_F	R^2_T	Significant fixed effects	Coefficient	S.E.	p-value	r^2
Dry Heath	log(*Calluna* +1)	plotID	0.332/ 0.296	0.429	Intercept	2.86	0.27		
					Year 2002 (vs. 2001)	-0.755	0.686	0.274	
					Year 2007 (vs. 2001)	-2.09	0.348	<0.001	**12.5%**
					Elevation	-0.006	0.001	<0.001	**6.5%**
					G1000	0.052	0.023	0.024	**-1.4%**
					2002: Elevation	-0.004	0.003	0.231	
					2007: Elevation	0.005	0.001	<0.001	**-6.5%**
					2002: G1000	0.297	0.119	0.015	
					2007: G1000	-0.052	0.03	0.089	**14.3%**
Alpine Heath	log(*Calluna* utilisation+1)	plotID	0.232/ 0.156	0.233	Intercept	1.75	0.358		
					Year 2002 (vs. 2001)	-0.349	0.304	0.257	
					Year 2003 (vs. 2001)	-0.689	0.288	0.021	**5.9%**
					Year 2008 (vs. 2001)	-0.747	0.288	0.012	
					DMB 2 (vs. DMB 1)	-0.946	0.313	0.005	
					DMB 3 (vs. DMB 1)	-1.08	0.306	0.001	**9.6%**
					DMB 5 (vs. DMB 1)	-0.892	0.333	0.012	
Species-rich Grassland	log(*Calluna* utilisation+1)	plotID	0.332/ 0.282	0.553	Intercept	2.37	0.401		
					Year 2008 (vs. 2001)	-2.31	0.519	<0.001	**5.7%**
					DMB 2 (vs. DMB 1)	-2.10	0.446	<0.001	
					DMB 3 (vs. DMB 1)	0.441	0.828	0.596	**9.5%**
					DMB 4 (vs. DMB 1)	-0.106	0.506	0.835	
					DMB 5 (vs. DMB 1)	-1.58	0.96	0.104	
					2008: DMB 2	2.42	0.573	<0.001	
					2008: DMB 3	-0.962	1.20	0.425	
					2008: DMB 4	0.782	0.664	0.244	**13.2%**
					2008: DMB 5	1.33	1.23	0.282	
					G1000	0.026	0.009	0.008	**3.7%**

Table 4.5b: Best fitting models for *Calluna* utilisation, deer density included in starting model, year excluded. DMB included only where significant in addition to deer density. The variance solely attributable to each fixed effect is shown in the final column (r^2).

Community	Response	Random effect	R^2_F/adjusted R^2_F	R^2_T	Significant fixed effects	Coefficient	S.E.	p-value	r^2
Dry Heath	log(*Calluna* + 1)	1|plotID	0.16/0.090	0.116	Intercept	1.151	0.321		
					DGCY	$1.56e^{-3}$	$6.94\ e^{-3}$	0.024	**0.1%**
					Elevation	$-2.47e^{-3}$	$8.24\ e^{-4}$	0.003	**3.0%**
					G1000	0.049	0.019	0.011	**4.3%**
Species-Rich grassland	log(*Calluna* + 1)	1|plotID	0.267/0.223	0.428	Intercept	-6.62	1.6	<0.001	
					DGCY	0.03	0.006	<0.001	**13.0%**
					DMB 2 (vs. DMB 1)	4.57	1.16	<0.001	
					DMB 3 (vs. DMB 1)	2.81	0.85	<0.001	**6.8%**
					DMB 4 (vs. DMB 1)	-3.31	0.815	<0.001	
					DMB 5 (vs. DMB 1)	5.42	1.47	<0.001	
					G500	0.025	0.010	0.009	**3.7%**

4.5 Discussion

Grazing impacts across all communities had reduced by 2007/8 compared with year of plot establishment (2001/2). Vegetation distribution patterns and elevation proved to be far better at explaining sward heights than deer density.

Elevation had important effects on the sward height of all of the heath communities, explaining between 5.9% and 17.5% of the variation, indicating climatic restriction on sward height. Increased utilisation was found on Wet and Dry Heaths in areas with high proportion of grassland, but this was not found on Alpine Heath. The effect of the proportion of preferred grassland on Species-Rich Grassland varied with scale: utilisation increased with more grassland at the smallest scale but more grassland at the largest scale had the opposite effect. Deer densities had some effect on *Calluna* utilisation on Species-Rich Grassland. Deer density explained negligible variance in sward height or *Calluna* utilisation on the three less preferred communities.

Effect of preferred grassland

The expectation that utilisation will be increased in areas with a high proportion of grassland was met for Wet and Dry Heaths, and partially met on Species-Rich grassland, although there were some contradictory results and the effect appears scale dependent. It was not met for Alpine Heath.

On Wet and Dry Heaths, more nearby *Agrostis-Festuca* grassland was associated with lower sward heights suggesting that the longer-term, average, grazing pressure on heaths away from community boundaries increased when there was more of the preferred community in the wider area. On Wet Heath the correlation was with grassland at the smallest scale (0-250 m), and it only explained 4% of the variance; on Dry Heath the correlation was with grassland 500-1000 m away and the effect was stronger, explaining 15% of the variation in sward height. There was also a significant positive correlation between grassland at this distance and utilisation of heather on Dry Heath, although the effect was not present in 2008 when overall utilisation was very low, with few non-zero values.

On Species-Rich grassland, grazing was increased (lower sward height and less litter) when there is more grassland within 250 m. *Calluna* utilisation was also positively correlated to proportion of grassland at the intermediate scale (250 – 500 m). These relationships only accounted for 2.7-5.2% of the variance in response variables, however.

A previous study found increased *Calluna* browsing near the boundary of dry heath-grassland communities when grassland was more abundant within 0.25km^2 (Palmer *et al.* 2003). I found that the effect of preferred community in modifying the grazing impact extended beyond the immediate vicinity of community boundaries.

An effect of the proportion of the preferred community within a few hundred metres on grazing on both the preferred and less preferred communities was found in a study of geese in the arctic (Speed *et al.* 2009); total browsing by moose has been found to be increased in areas of higher productivity, at scales from 0.8km^2-25km^2 (upper limit was comparable with home range size) (Månsson *et al.* 2007).

Curiously, on Alpine Heath and Species-Rich Grassland there was a positive relationship between sward height and the proportion of *Agrostis-Festuca* grassland at the largest scale addressed (500 – 1000 m away). This was contrary to expectations, as it indicates lower grazing pressure in the presence of more grassland at this scale. On Species-Rich Grassland this accounted for 9.0% of the variance in inter-tussock height.

As the survey was carried in summer, so grasslands are not likely to be utilised to their full capacity (Gordon 1989c), so it is not surprising that there should be some variation in utilisation. Increased sward height on Species-Rich Grassland where there was more preferred grassland between 500 and 1000m away possibly occurred because deer with more grassland in their home range spread their grazing over all grassland within the home range, dissipating impacts on the preferred community, whereas deer with little grassland in their home range will be concentrate their grazing on these smaller areas of grassland. This can only occur if deer home ranges are distributed unevenly with respect to resources (i.e. do not conform to the ideal free distribution (Fretwell & Lucas 1969)), which is likely in this system. Red deer, and especially hinds, have fixed home ranges as adults, and hinds do not disperse far from their natal range, so will not distribute themselves evenly with respect to resources. Stags do disperse, but as the deer are culled, the distribution is likely to remain uneven, rather than dispersal balancing it out in the long term (Clutton-Brock *et al*. 1982).

Why the same negative correlation between grassland and Alpine Heath sward height occurs is possibly because many plots were intermediate between heath and grassland community types, and so perhaps they become the preferred community type, where there is little grassland within the vicinity.

Effect of deer densities and deer management block

Deer density or deer km^{-2} grassland was not significant or explained a negligible proportion of variance in sward height on Wet and Dry heath, and only 3.2% on Alpine Heath. Furthermore, the relationship between sward height and deer density on Dry Heath counter-intuitively indicated increased sward height when more deer were present. On Alpine Heath and Species-Rich Grassland, differences between deer block were significant, indicating that there were other underlying differences at this scale that were also important. On Alpine heath, DMB differences and explained far more variation than deer density, indicating that these differences were of more importance than deer density.

Deer km^{-2} of grassland was able to account for 13.0% of the *Calluna* utilisation Species-Rich Grassland, but was unimportant in explaining *Calluna* utilisation on the three Heath communities.

Given the coarse temporal scale of the deer counts they may not accurately represent the average deer pressure in the block over the whole year. However, infrequent, large-scale counts are often the level of information that is available for deer management units. Other studies have drawn mixed conclusions about the utility of large scale deer counts in predicting local impacts: although (Albon *et al.* 2007) found relationships between estate level deer densities and measures of herbivore impact; Palmer *et al.* (2003) did not, whereas (Mysterud *et al.* 2010) measured browsing levels on three plant species and found a relationship with large scale deer density for only one species.

The differences in found between deer blocks cannot be attributed to any particular factor, as overall there was no consistent pattern in differences between DMBs. It was clear that the differences were not entirely due to deer densities, since DMB was fitted in addition to deer density in some models. Due to a long term no-cull policy, DMB 4 had an exceptionally high number of deer relative to grassland area (Table 2); however, it did not have exceptional leverage in the models. It might also be expected that DMB 2 would stand out as having higher utilisation than expected for the deer density in the area, because of the presence of other herbivores (goats, cattle and ponies all present in this block), and especially on heather and on heath communities because of the presence of goats. DMB 1 has a similar number of goats to DMB 2 (see Appendix V for location of goats in 2010). However, the pattern of differences between blocks does not appear to reflect this. On both Species-Rich Grassland and Alpine Heaths when a measure of deer density is included in the model, sward height is in fact lower in DMB 2, but also DMB 5, where goats are rarely found. With deer density in the model, *Calluna* use on Species-Rich Grassland is higher than expected in DMB 2 and 5. It is likely that systematic differences in climate and topography between DMBs are also contributing.

Conclusions and Management implications

The findings of the study have broad implications for managing landscapes of protected communities containing both grazing intolerant communities and communities dependent on grazing to maintain their favourable characteristics.

The results suggest that in areas where there is a lot of the preferred community, the less preferred communities are more heavily used, since these are less tolerant of grazing in the study system, this increases the possibility of conflict in management in such areas. In this system the effect appears particularly important for Dry Heath, where the scale at which grassland area had the most influence was 500-1000 m. We also found that grasslands were less used in these areas where there was more grassland at 500 – 1000 m (although the effect size was smaller), which will exacerbate conflict in management in such areas. The taller sward heights on grassland in such areas indicates that they are more likely to become grazed at sub-optimal levels, leading to a loss of the low-growing herbs that earn the community its designation as a protected NATURA community (MacDonald *et al.* 1998b, Britton & Pakeman 2009). Decreased grazing pressure on the preferred resource when it is abundant will only occur when herbivores are distributed unevenly with respect to preferred food resource: aggregation of herbivores is common, and many reasons other than preference for one vegetation community contribute (Fryxell 1991). Hefting to home range and the advantages of foraging on heavily used grazing lawns are two factors applicable to deer and other herbivores that show similar group foraging behaviour.

The lack of effect of deer density on the utilisation of heath suggests that most of the variation in utilisation on the less preferred communities is at a smaller scale, at least over the range of deer densities in this system, and is driven more by the influence of in the location of the preferred community on herbivory.

There was still much variation unaccounted for by the large scale factors included in the models, however, it is common for large scale patterns in browsing or grazing pressure to be influenced by many factors, each explaining a small proportion of the variation (e.g. Månsson *et al.* 2007, Mysterud *et al.* 2010). In my study system, variation in local community composition is one such probable 'missing' factor. Community composition has previously been found to be of importance to the selection of grassland by deer (Bellu *et al.* 2012), and high and low diversity varieties of *Agrostis-Festuca* grassland experience slightly different degrees of selection by herbivores on Rum (Gordon 1989b). Other factors could include variation in soil types and spatial variation in vegetation community layout that was below the resolution of available data. *Calluna* utilisation is sensitive to very local phenomena not recorded in this study, e.g. the presence of deer paths, and this could be having an effect on some sites (Oom & Hester 1999). Since the heath plots in this study are quite varied in composition, including varying proportions of grasses, sedges and herbs alongside dwarf shrubs, small scale selection within the community was also likely to be contributing to variation in *Calluna* utilisation.

Predictions of browsing patterns need to combine vegetation data with information on other factors known to influence habitat use such as abiotic factors related to shelter, topography and weather conditions (e.g. Mysterud *et al.* 2010, Månsson *et al.* 2012), and (where present) predation risk and human disturbance (Bailey & Provenza 2008). Browsing patterns differ seasonally as different influences become more important, e.g. depletion of preferred forage in winter and changes in weather conditions leading to altered preferences for forage type and for certain elevations (e.g. Bailey & Provenza 2008, van Beest *et al.* 2010b). Ideally, year round patterns of grazing pressure should be considered.

Managing the numbers of grazers at a coarse scale in a complex landscape containing communities with different grazing requirements is always going to involve compromise as management targeted at preserving one type of community is likely to be sub-optimal for others in certain areas of the landscape. The spatial layout of the communities, as well as other factor such as the availability of shelter, will act to concentrate animals in certain areas of the landscape. On the other hand this spatial variation in grazing impact may in some ways be desirable, as it will allow at least some area of grazing-dependent communities to be maintained in good condition in areas of high impact, without threatening vulnerable communities at the rest of the site. Understanding how vegetation distribution and other abiotic and biotic factors control the impact of grazing on different plant communities in different areas is essential information for managers in determining which areas are most likely to have conservation goals compromised. In turn this will allow a decision to be made on whether to implement finer scale management or to accept the compromise. Whilst very fine scale selection of species and habitats at anything below a few hectares in scale cannot be directly addressed by management measures, areas of priority habitat identified as generally vulnerable because of the landscape context (several ha to km^2) might be targeted for further monitoring and possible micromanagement using fencing or grazing with managed domestic stock that allow some finer control of grazing pressures than free ranging herbivores.

Chapter 5: Effect of landscape-scale vegetation patterns on grazing impact: application to a combined index of grazing impacts

5.1 Summary

- Many plant communities of conservation importance are managed using large herbivores; spatial variation in grazing intensity can complicate management planning. Many factor influence the distribution of accumulated grazing or browsing pressure at large scales, understanding the influences of these pressures can aid management decisions.
- The distribution of high qualit y food resources can affect impact grazing distribution at multiple scales.
- Using similar approach to that of Chapter 4, I analyse a dataset which was collected from the same geographic area but used a different measure to assess grazing impacts. Data was collected from four different plant communities of conservation value (Species-rich grassland (SRG); Blanket Bog; Dry Heath; Wet Heath). Species-rich grassland is the preferred plant community for the main herbivore present (red deer).
- The variance explained by the proportion of SRG within 1km and deer density was calculated and used to assess its importance for grazing patterns on preferred and less preferred communities.
- Grazing impacts on the less preferred communities are positively correlated with proportion of the less preferred community in the locality, which explains 11- 16% of the variance.
- Unexpectedly, there is a negative correlation between the proportion of preferred community within 1km and the grazing impacts on SRG, but the effect size is small.
- Local deer density is positively correlated with grazing impact on Grassland and Dry Heath. However the effect size is small on Dry Heath. The effect size of deer density on SRG could not be accurately determined as it was almost wholly confounded with the effect of Elevation.

- The results of this chapter are in broad agreement with the results of the preceding chapter, despite the differences in measures of grazing impacts used. The results suggest that conflict in management for different community types in this system is most likely to occur in areas where there is a high proportion of the preferred community within the local area. In these areas, excessive grazing of less preferred communities is likely.

5.2 Introduction

Herbivory is distributed unevenly across the landscape, at many spatial scales (Bailey *et al.* 1996); understanding the causes and consequences of spatial heterogeneity in grazing is of importance to setting appropriate stocking levels to achieve management aims in heterogeneous landscapes (Bailey *et al.* 1998, Stalmans *et al.* 2001, Ebrahimi *et al.* 2010).

The abundance and distribution of food resources is an important influence on herbivore distribution. Marginal value theorem (MVT) predicts that herbivores will select their grazing areas for high quality resources, and switch to low quality resources when either the high quality resource is depleted, or when the energetic cost of searching for or travel to a high quality patch is prohibitive (Charnov 1976). Large grazing herbivores generally have a continuous resource of varying quality, rather than distinct patches as assumed by MVT; however, they are able to distinguish food resources of different quality at varying scales (Duncan *et al.* 1994, Searle *et al.* 2006) (from individual plants or plant parts up to different community types), and travel costs can be an important part of a herbivore’s energy budget, and thus affect foraging strategy (Murray 1991, Oom *et al.* 2010). Grazing on a usually less preferred (low quality), but nearby, resource patch may be more energetically efficient than travelling to a distant preferred (high quality) patch. This leads to the prediction that grazing intensity will be higher on low quality resources that are in close proximity to high quality ones compared to low quality resources elsewhere, and grazing should also be lower on high quality resources when they are isolated from other high quality resources.

Increased grazing on a lower quality resource in proximity to a high quality one has been found at small scales for large herbivores grazing two-community mosaics: on an artificial grassland the consumption of the low quality species was elevated within 1-5 m of a high quality patch (Dumont *et al.* 2002), and on a heath-grassland mosaic, browsing on heather is elevated within 5 m of the boundary with grassland (Clarke *et* *al.* 1995b, Oom *et al.* 2010). The effect can also be observed on patterns of browsing intensities on individual species: browsing on less preferred tree species is elevated in stands containing a high proportion of the most preferred species (Barbosa *et al.* 2009, Milligan & Koricheva 2013); the opposite effect, where preferred species are browsed less in areas with a high proportion of unpalatable species is also sometimes observed (Bee *et al.* 2009).

Herbivores selecting feeding areas at large scales (but within home range) are constrained by multiple factors (Senft *et al.* 1987, Bailey *et al.* 1996), consequently food resources may become less important as a determinant of the spatial distribution of grazing as scale increases. There has been less research into whether the abundance and distribution of food resources influences the spatial pattern of grazing on high and low quality food resources at larger scales (up to home range size). Two such studies found that the proportion of the preferred vegetation community was positively correlated with utilisation of the less preferred community (Palmer *et al.* 2003, Speed *et al.* 2009). Utilisation of the preferred community was also increased in areas with a high proportion of the preferred community, in the one study that tested this (Speed *et al.* 2009). Other studies have addressed the effect of some aspect of habitat quality other than the proportions of each food type: habitat productivity was found to be correlated with increased total moose (*Alces alces*) browsing, the effect size varied with scale, and was more important at the largest scales studied (Månsson *et al.* 2007). In a study of red deer (*Cervus elaphus*) browsing, however, the effect of habitat productivity was non-linear and varied between different species of browse (Mysterud *et al.* 2010).

The impact of large herbivores is a major influence on many plant communities of conservation importance (Wallis De Vries 1998, Rook *et al.* 2004, Halada *et al.* 2011, Rosenthal *et al.* 2012). Many of these are grazed by wild or free-ranging herbivores (Gordon *et al.* 2004). When managing a mixture of different community types that differ in their grazing requirements, conflicts in management may occur across large scales (Holland *et al.* 2010). This could be caused by, or increased by the attraction of herbivores to particular plant communities, resulting in elevated grazing on adjacent communities. However, to date studies of the role of community layout in contributing to the distribution of grazing patterns have been largely limited to small scale studies, with the exceptions of those discussed above (Palmer *et al.* 2003, Månsson *et al.* 2007, Speed *et al.* 2009).

Taking a similar approach Chapter 4, the goal of this study was to assess the importance of the effect of:

a) the proportion of the preferred community in the locality at three spatial scales, and

b) the local deer density

on the distribution of grazing on four plant communities of conservation value in a complex mosaic. The plant communities included were the preferred community (Species-Rich Grassland) and three less preferred plant communities (Dry Heath, Wet Heath and Blanket Bog). I predicted that a higher grazing impact will be found on all communities where there is a higher proportion of the preferred community. I also predicted that higher impacts on all communities should be found at higher deer densities. The implications of the results for the likelihood of conflict in managing the different communities in this study are then discussed.

5.3 Methods

Data

The study site was the Isle of Rum (57^0 00'N, 6^0 22' W), which is described more fully in Chapter 4 and Chapter 1 (section 1.3). The Isle of Rum is particularly suitable as a study site for the possible occurrence of management conflict on the following basis: several communities of conservation importance are present; there is evidence of considerable variation in grazing impacts around the island; and although the grazing-dependent community is also the preferred community for grazers, there is evidence of conflict in management for the different communities in that the grazing-dependent species-rich grassland is showing signs of under-grazing (Dayton 2008, Britton & Pakeman 2009) whereas the less grazing tolerant heath communities are still, according to some surveys, being overgrazed in places (Dayton 2008, Dayton 2011).

We used the results of a 2008 'Habitat Impact Assessment' (HIA) survey (Dayton 2008) to examine the relationship between grazing impact and landscape variables. Results were analysed for four plant community types: Blanket Bog, Dry Heath, Wet Heath and Species-rich grassland (SRG). All communities are of international conservation importance, listed in Annex 1 of the Habitats Directive (Council of the European Communities 1992). SRG is the community preferred by the grazers and needs grazing to maintain its species richness. The other communities are vulnerable to too much grazing.

The HIA produces a grazing impact score, on a continuous scale from 1 (low) to 3 (high impact), calculated from the average of several grazing indicators which are each scored on a discrete scale (1 = Low, 2 = Moderate and 3 = High). The grazing score has different implications for each plant community type, as they have different grazing requirements; the range of acceptable impact (from SNH) for these communities is shown in Table 5.1. Grazing impacts outside these ranges would be classed as ‘over-’ or ‘under-grazing’. The indicators of grazing that contribute to the overall impact score are listed in Table 5.1. The score of each indicator is equated to a number and the average is calculated. Full details of the methodology can be found in MacDonald *et al.* (1998a).

The locations of the sampling points were determined by stratified random selection. Within each of five deer management blocks (Fig 5.1), 28 locations were randomly generated for each of the four plant community types, based on polygons from a previous National Vegetation Classification survey. However, not all points were surveyed due to access problems or inaccuracy of vegetation mapping. The locations of the sampling points that were surveyed are shown in Fig 5.1.

Table 5.1: Grazing impact indicators and acceptable impact ranges for the Blanket Bog and Dry and Wet Heaths. From (MacDonald *et al.* 1998a), where more complete descriptions of indicators can be found. The acceptable impact range for each habitat i.e. the range which is not likely to cause any deterioration of habitat is shown as range on numeric scale and as a description on an ordinal scale. L=Low; LM = Low/Moderate; M=Moderate; MH = moderate-High; H = High.

Plant community	**List of grazing impact indicators**	**Indicator level**			**'Acceptable' impact According to SNH**	
		H	**M**	**L**	**Numeric scale**	**Descriptive scale**
Blanket Bog	Browsing on less palatable shrubs: (*Erica tetralix, Arctostaphylos uva-ursi, Empetrum nigrum, Vaccinium vitis-idaea*)	Some	-	None	1-1.749	L-LM
	Rubus chamaemorus flowering /fruit	Majority of shoots with no flowers/ fruit.	-	Majority of shoots flowering/fruiting.		
	Eriophorum vaginatum flowering	Little or none	Patchily abundant or widespread but thinly scattered	Widespread and abundant		
	Myrica gale growth form and browsing	Browsed shoots conspicuous, easy to find. Dense branching	Browsed shoots easy to find, less immediately conspicuous. Variably dense branching	Browsing difficult to find/absent Even, regular branching		
	Dung	Easy to find	-	Rare & difficult to find		
Dwarf shrub heath (including Dry and Wet Heath)	Browsing on less palatable shrubs *Erica tetralix*, *Arctostaphylos uva-ursi, Empetrum nigrum.*	Some	-	None	1-1.749	L-LM
	Browsing on long shots of *Calluna vulgaris/ Vaccinium myrtillus*					
	a) Where plants moderately vigorous (shoot growth >4cm yr^{-1})	>66%	33-66%	<33%		
	b) Where plants less than moderately vigorous	>33%	16-33%	<16%		
	Flowers/fruit on *Calluna/ Vaccinium myrtillus*	Sparse	Obvious but patchy	Abundant and conspicuous		
	Summer browsing on *Calluna*	Extensive	Limited, patchy	Limited, patchy		
	Type of shoot material removed	Woody shoot browsed frequently	Little/no browsing of woody shoot older than 1 yr	Only tips of shoots browsed		

Table 5.1 cont.: Grazing impact indicators and acceptable impact ranges for Species-Rich Grassland. From (MacDonald *et al.* 1998a)

Plant community	**List of grazing impact indicators**	**Indicator level**			**'Acceptable' impact According to SNH**	
		H	**M**	**L**	**Numeric scale**	**Descriptive scale**
Species-rich grassland (SRG)	Sward Height	<3cm	3-6cm	>6cm	1.25-2.749	LM-MH
	Uprooted bundles of grass tillers	Abundant	-	Sparse/Absent		
	Litter	<1cm layer	1-3cm	>3cm		
	Signs of grazing on unpalatable herbs	>10%	<10%	Few/ no leaves grazed		
	Grazing on legumes	Extensive	Frequent	Sparse/absent		
	Flowering of grasses and herbs >3cm	Sparse/none	Scattered	Abundant		
	Grazing broad leaved grasses	All/nearly all grazed	>50% but ungrazed leaves easily found	<50%		
	Grazing on fine grasses	>66%	33-66%	<33%		
	Signs grazing on *Deschampsia cespitosa*	>15%	<15%	Little/none		
	Cover of mosses	>50%	<50% but present	Not obvious		
	Saplings >5cm tall	Absent	-	Present		
	Breakage and uprooting small herbs	>20%	10-20%	<10%		
	Density of shoots of alpine cushion plants and 'weeding' (uprooting) of grasses from cushions	Dense cushions, extensive weeding	-	Loose cushions. No weeding		

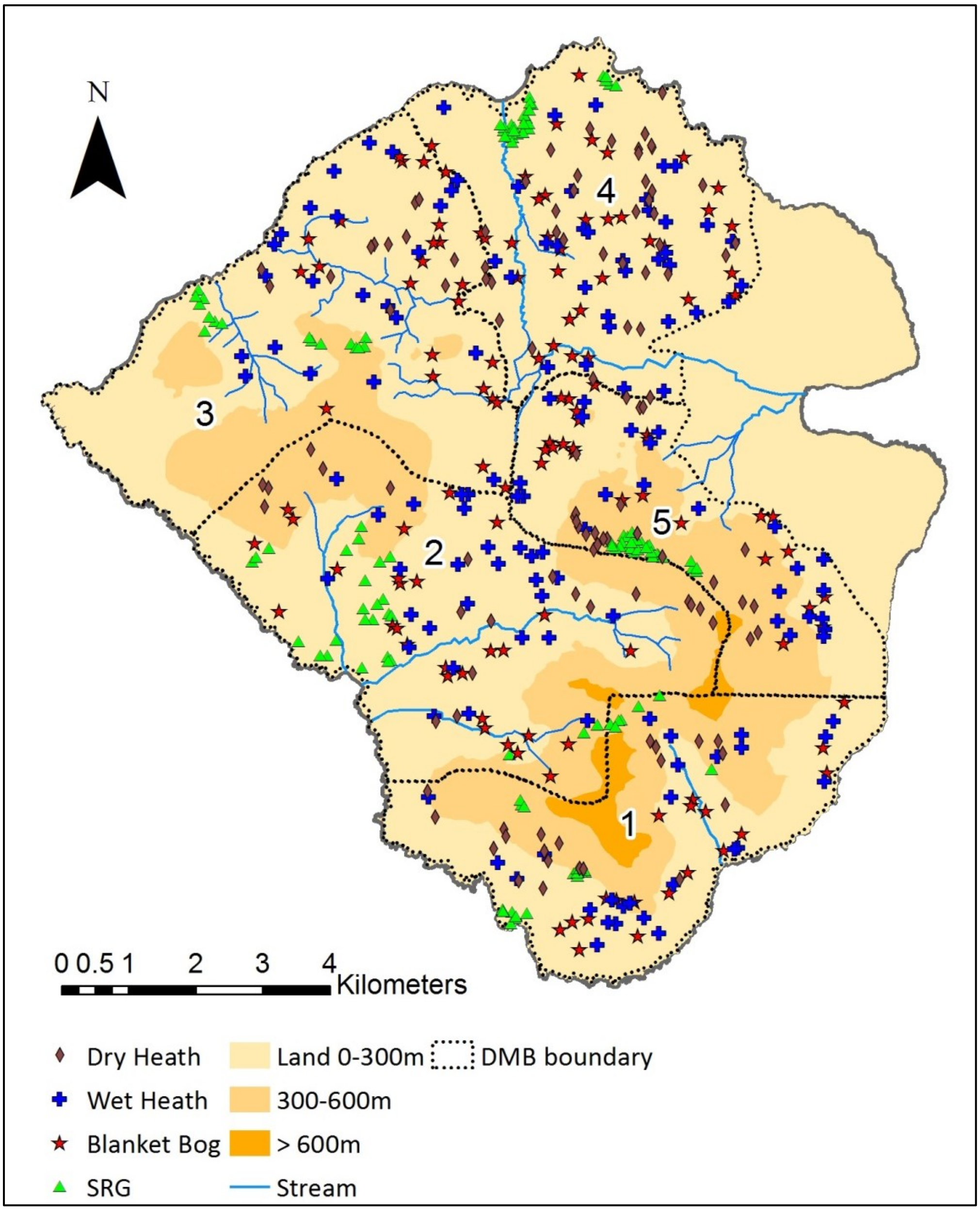

Fig 5.1: Location of sampling sites on Isle of Rum. The five numbered areas are deer management blocks (DMBs). The unmarked area in the east of the island is largely woodland and no sampling points are located within this area.

Statistical analysis

All analyses were carried out in R 3.0.3 (R Core Team 2013). I tested whether utilisation measures were associated with: micro-climate (Elevation); the percentage *Agrostis-Festuca* grassland within three concentric rings, 0-250 m, 250 – 500 m and

500 – 1000 m (abbreviated hereafter to G250, G500 and G1000, respectively); and deer management block (DMB - as a categorical explanatory variable). The definition of *Agrostis-Festuca* grassland and means of calculating the proportion present is described in Chapter 4. The full model was:

$y \sim DMB + E + G1000 + G500 + G250$ eqn 1

Where y was the grazing impact index; E=elevation; G1000, G500, G250 were the effects of the percentage *Agrostis-Festuca* grassland present within the three concentric rings. From the full model, stepwise model simplification was carried out by deletion of non-significant terms. To investigate the role of deer density, the analysis was repeated with deer density and deer km^{-2} *Agrostis-Festuca* grassland. These were calculated as in Chapter 4: deer density (abbreviated to D08 in tables of results) was calculated for each of five management blocks on the island (the smallest scale for which data was available) from the numbers counted in the annual Deer Commission for Scotland deer count. The deer km^{-2} *Agrostis-Festuca* grassland (abbreviated to DG08 in tables of results) was calculated based on the total area of *Agrostis-Festuca* grassland (as defined in Chapter 4) in the block.

Partitioning of the variance explained by the final models containing only significant variables was carried out using the method described by Mood (1969) based on the model R^2 value, in order to assess the importance of the relationships found. The variances uniquely attributable to each explanatory variable (unique effect) and to the combined effects of two or more variables (common effects) were calculated. Common effects occur when there is co-linearity between the explanatory variables and these overlapping effects can make either a positive or negative contribution to total model R^2 (see Seibold & McPhee 1979 for further details). Positive common effects occur when two (or more) explanatory variables explain the same portion of the variation in the response variable. Negative common effects can occur when explanatory variable (X1) is collinear with some part of another explanatory variable (X2) that is orthogonal to the response variable (Y); in other words the inclusion of X1 increases the contribution of X2 to explaining Y because it cancels out the irrelevant part of X2 see (see Beckstead 2012 for a more thorough discussion of the causes and consequences of negative common effects).

Residuals plots were checked for trends to check that the assumption of normality and independence of variance was upheld. Final models were refitted with generalised least squares modelling using package nlme (Pinheiro *et al*. 2012) to enable testing of residuals for spatial autocorrelation. Spatial autocorrelation in residuals was assessed by computing Moran's I correlograms using the 'correlog' function in package ncf (Bjornstad 2013). The significance of whole correlogram is assessed by Bonferoni correction: comparing the p-values for each distance class against a corrected p-value.

5.4 Results

Overall grazing status

A substantial proportion of survey points on Blanket bog, Dry and Wet Heath communities had scores in the range that are classed as overgrazing (score ≥1.75) (Fig 5.2), (Blanket Bog = 47.7%; Dry Heath = 23.7%; Wet Heath = 26.7% of data points). Conversely, 13.4% of SRG survey points were classified as under-grazed (<1.25), and only three sites (2.3% of data points) as overgrazed (≥2.75) (Fig 5.2).

Effect of proportion of preferred community within 1km

On all three of the less preferred communities (Blanket Bog, Dry Heath and Wet Heath), grazing impact score was positively correlated with the proportion of grassland within 1km. (Fig 5.4, Tables 5.2, 5.3, 5.4)

For Blanket Bog, the correlation was with the proportion of grassland within 500 – 1000 m in the models including deer per km^2 and DMB (Table 5.2). The model with DMB included explained the most variance in total (20.4%); in this model, proportion of grassland within 500 – 1000 m explained 12.3% variance. Grassland within 500 – 1000 m had the best fit in the model with deer density (Table 5.3), where it explained slightly more variance than grassland within 500-1000 m in the other models (13.4%) (Fig 5.4).

On Dry Heath there is a positive correlation was found with the proportion of grassland within 500 – 1000 m (Table 5.2; Table 5.3), which explained 14.2% variance. When deer density was not included in the model there was also significant, negative correlation with grassland within 250-500 m and grassland 500-1000 m away explained a slightly larger proportion of the variance (15.8%). Commonality analysis showed that the main contribution of grassland within 250-500 m to the result was a negative common effect with grassland 500-1000 m away. Its positive contribution to explained variance was only 2.3%. The variable of grassland 250-500 m away was mainly acting as a suppressor variable.

Wet Heath there was a positive correlation with the proportion of grassland within 250 – 500 m (Table 5.3; Table 5.2), which explained 13.3% of the variance (Fig 5.4).

On Species-rich Grassland (SRG), the proportion of grassland within 500 – 1000 m was negatively correlated with grazing impact in all three model runs (Table 5.2; Table 5.3; Table 5.4) though the total positive contribution to variance was low (6.3% at most) and some of this was confounded with deer density and DMB in the models with these variables present (Fig 5.4).

Differences between DMBs

There were significant differences in grazing impact between DMBs on Blanket Bog and Dry heath which did not appear to be related to deer densities. The Blanket Bog model including DMB explains 8.0% more variance than that containing grassland area alone, which is a greater improvement to the model than the addition of deer km^{-2} of *Agrostis- Festuca* grassland. On Dry Heath, the difference between DMBs explained more variance (27.7%) than the combined effect of deer density and proportion of grassland (18.9%) (Table 5.2, Fig 5.3). On SRG, the explanatory power of DMB appears to be mostly due to the differences in deer density, as it explains a similar proportion of variance (Fig 5.3).

Effect of deer density

Grazing impact score was not correlated with deer density on either Blanket Bog or Wet Heath. Deer density the level of management block was positively correlated with grazing impact on Dry Heath (Table 5.3; Fig 5.5), where it explains 5.2% of the variance (Fig 5.3). It was also positively correlated with grazing impact on SRG (Table 5.3; Fig 5.5), but the effect was largely confounded with the effect of elevation (Fig 5.3). Elevation is negatively correlated to both grazing impact on SRG and to deer density ($R^2 = 0.34$), and 23.9% of variance in grazing impacts on SRG could not be attributed solely to either factor but to the common effect of both. Only 1.6% variance can be attributed to deer density alone.

Grazing impact scores on Blanket Bog were correlated with the number of deer km^{-2} of *Agrostis-Festuca* grassland, explaining only 2.3% variance after the negative common effect with grassland is subtracted (Table 5.4; Fig 5.3). Grazing impact score was not correlated with deer km^{-2} of *Agrostis-Festuca* grassland on Dry Heath, Wet Heath or SRG (Table 5.4).

Model residuals

No significant spatial auto correlation was found in model residuals. Blanket Bog residuals values became more positive at higher values of the grazing impact score.

Residuals from all other models met assumptions of normality and equal variance adequately.

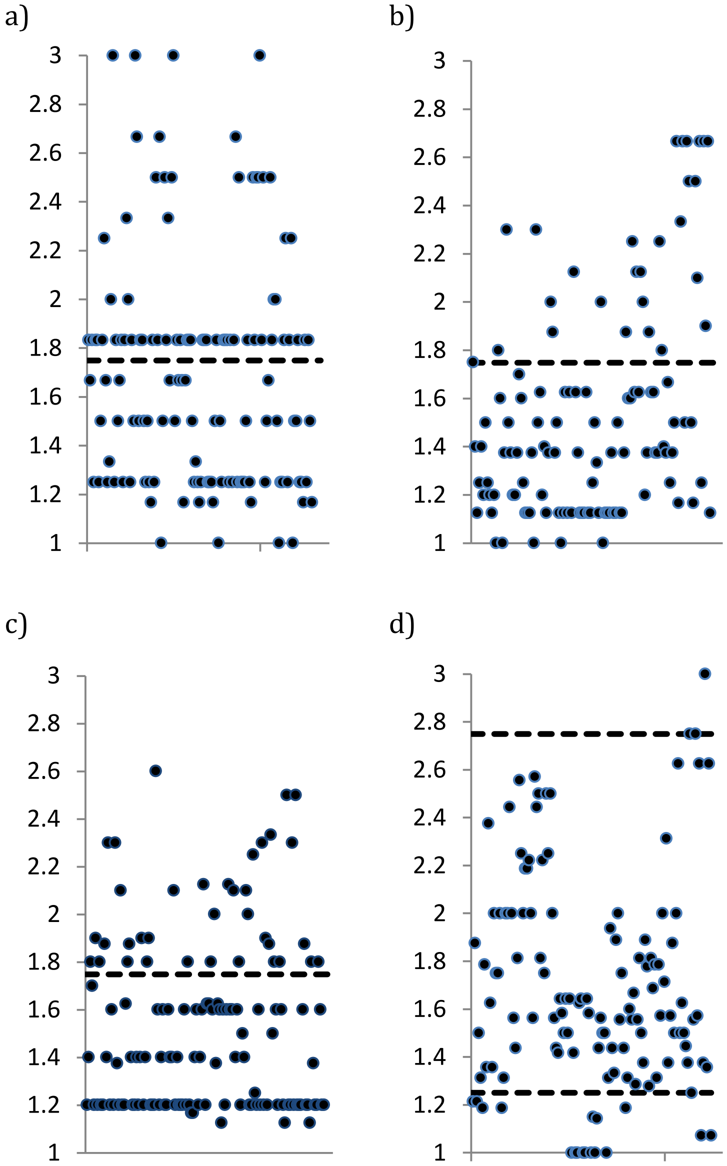

Fig 5.2: Distribution of grazing impact scores on a) Blanket bog; b) Dry Heath; c) Wet Heath; d) SRG. The dashed lines on a, b, and c show scores above which the point was classed as overgrazed, d also shows the limit below which plots were classed as undergrazed.

Table 5.2: Final models resulting from the full models with DMB fitted in the full model. Response variable is grazing impact score. DMB = Deer management block; E=elevation; G250, G500, G1000 = percentage *Agrostis-Festuca* grassland within 0 – 250 m, 250 – 500 m and 500 – 1000 m, respectively.

Community	**Model adjusted R^2**	**Significant factors in final model**	**Coefficient**	**S.E.**	**P-value**
Blanket bog	**0.204**	Intercept	1.32	0.106	
		DMB 2 (v. DMB 1)	0.213	0.129	0.101
		DMB 3 (v. DMB 1)	0.331	0.130	**0.012**
		DMB 4 (v. DMB 1)	0.496	0.129	**<0.001**
		DMB 5 (v. DMB 1)	0.123	0.129	0.343
		G1000	3.89 e^{-2}	8.64 e^{-3}	**<0.001**
Dry Heath	**0.281**	Intercept	1.96	0.083	
		DMB 2 (v. DMB 1)	-0.251	0.119	**0.036**
		DMB 3 (v. DMB 1)	-0.623	0.124	**<0.001**
		DMB 4 (v. DMB 1)	-0.544	0.107	**<0.001**
		DMB 5 (v. DMB 1)	-0.665	0.111	**<0.001**
Wet Heath	**0.133**	Intercept	1.45	0.033	
		G500	0.038	0.0082	**<0.001**
SRG	**0.425**	Intercept	2.32	0.113	
		DMB 2 (v. DMB 1)	-0.207	0.116	0.078
		DMB 3 (v. DMB 1)	-0.283	0.108	**0.010**
		DMB 4 (v. DMB 1)	-0.169	0.120	0.163
		DMB 5 (v. DMB 1)	-0.227	0.109	**0.040**
		G1000	-0.015	0.0061	**0.014**
		Elevation	-1.45e^{-3}	2.79 e^{-4}	**<0.001**

Table 5.3: Final models resulting from the full models with deer km^{-2} fitted (only shown if differing from final models in Table 5.2, above), showing significant fixed effects and total model adjusted R^2. The response variable is grazing impact. D08 = Deer density (at the level of DMB) in 2008. Other abbreviations as Table 5.2, above).

Community	**Model adjusted R^2**	**Significant factors in final model**	**Coefficient**	**S.E.**	**P-value**
Blanket bog	**0.123**	Intercept	1.47	0.032	
		G500	0.023	0.005	**<0.0001**
Dry Heath	**0.189**	Intercept	1.14	0.093	
		D08	0.023	0.007	**0.002**
		G1000	0.042	0.009	**<0.0001**
SRG	**0.416**	Intercept	1.92	0.133	
		D08	1.63 e^{-2}	7.80 e^{-3}	**0.038**
		G1000	-1.40 e^{-2}	-1.39 e^{-2}	**0.002**
		Elevation	-1.22 e^{-3}	2.10 e^{-4}	**<0.0001**

Table 5.4: Models with deer km-^{2} *Agrostis-Festuca* grassland fitted (where differing from above). The response variable is grazing impact. DG08 = Deer per km^{-2} *Agrostis Festuca* grassland (at the level of DMB) in 2008. Other abbreviations as Table 5.2, above).

Community	**Model adjusted R^2**	**Significant factors in final model**	**Coefficient**	**S.E.**	**P-value**
Blanket Bog	**0.148**	Intercept	1.436	0.077	
		DG08	6.89 e^{-4}	2.70 e^{-4}	**0.012**
		G1000	3.58 e^{-2}	7.68 e^{-3}	**<0.001**
Dry Heath	**0.164**	Intercept	1.372	0.052	
		G1000	0.059	0.012	**<0.001**
		G500	-0.023	0.010	**0.030**
SRG	**0.400**	Intercept	2.17	0.065	
		G1000	-1.62 e^{-2}	4.37 e^{-3}	**<0.001**
		Elevation	-1.50 e^{-3}	1.65 e^{-4}	**<0.001**

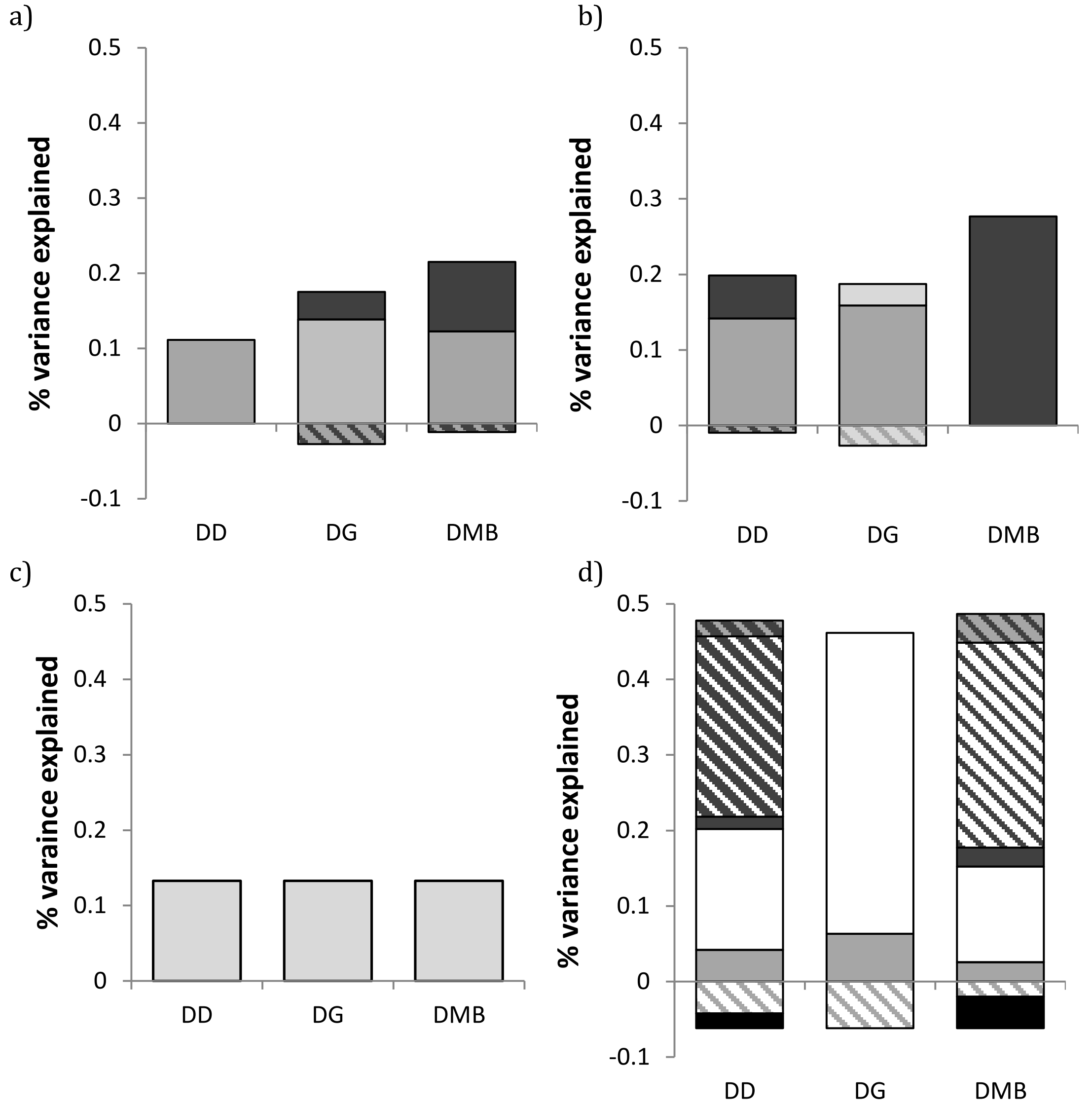

Fig 5.3: Grazing impact models for each community: contribution to explained variance of significant model factors. DD= model including deer density. DG= model including deer per km^2 *Agrostis-Festuca* grassland. DMB =model including DMB. a) Blanket bog b) Dry Heath c) Wet heath; d) SRG. □= Elevation ■ = DMB / Deer density/ Deer per km^2 *Agrostis-Festuca* grassland; ▩ = G1000▢ = G500; ◩ = variance common to two factors; ■=variance common to three factors

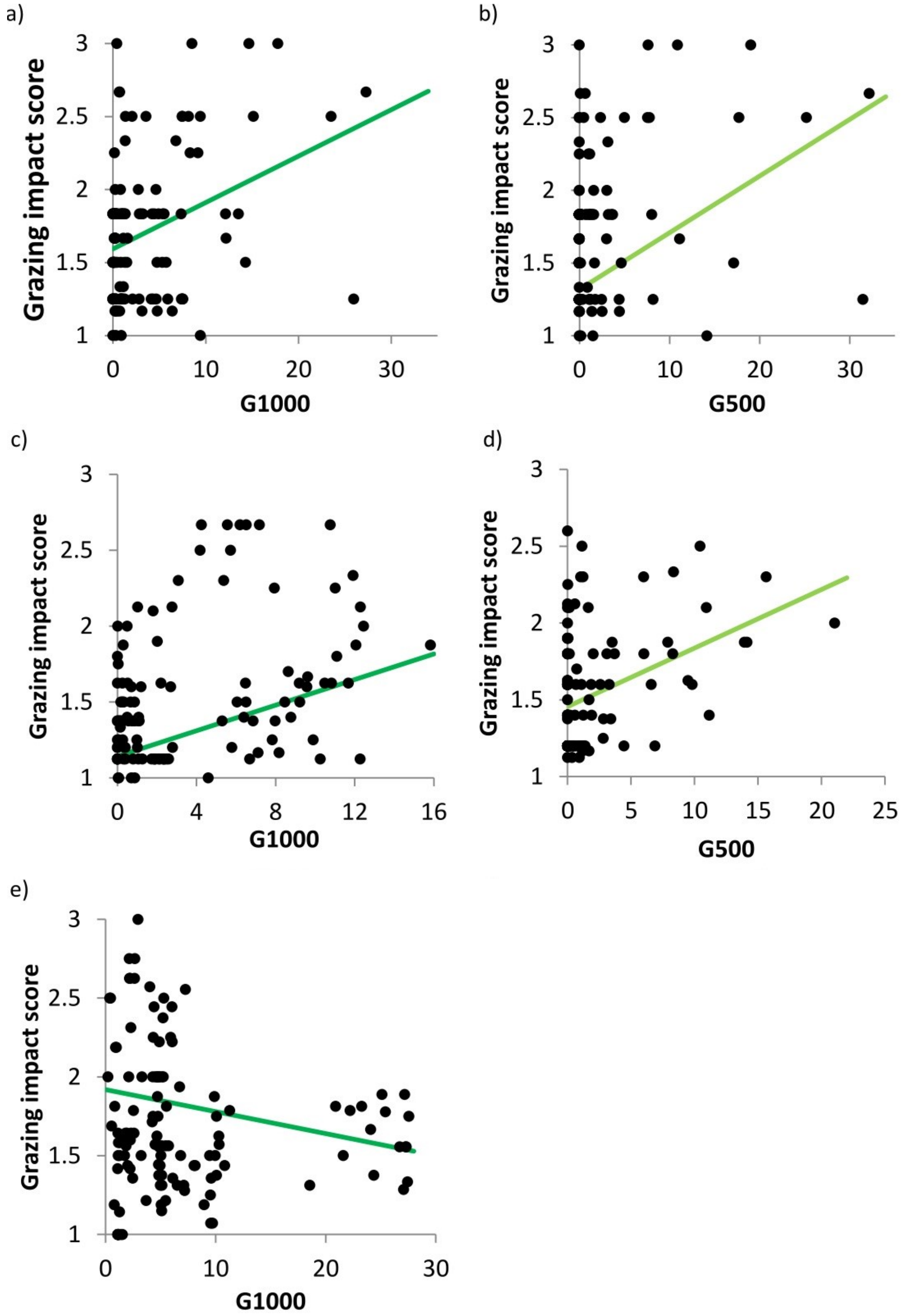

Fig 5.4: Fitted relationship between grazing impact score and proportion grassland. Abbreviations as Table 5.2, above. a) Blanket bog (Table 5.2) b) Blanket bog (Table 5.3) c) Dry Heath d) Wet heath; e) SRG.

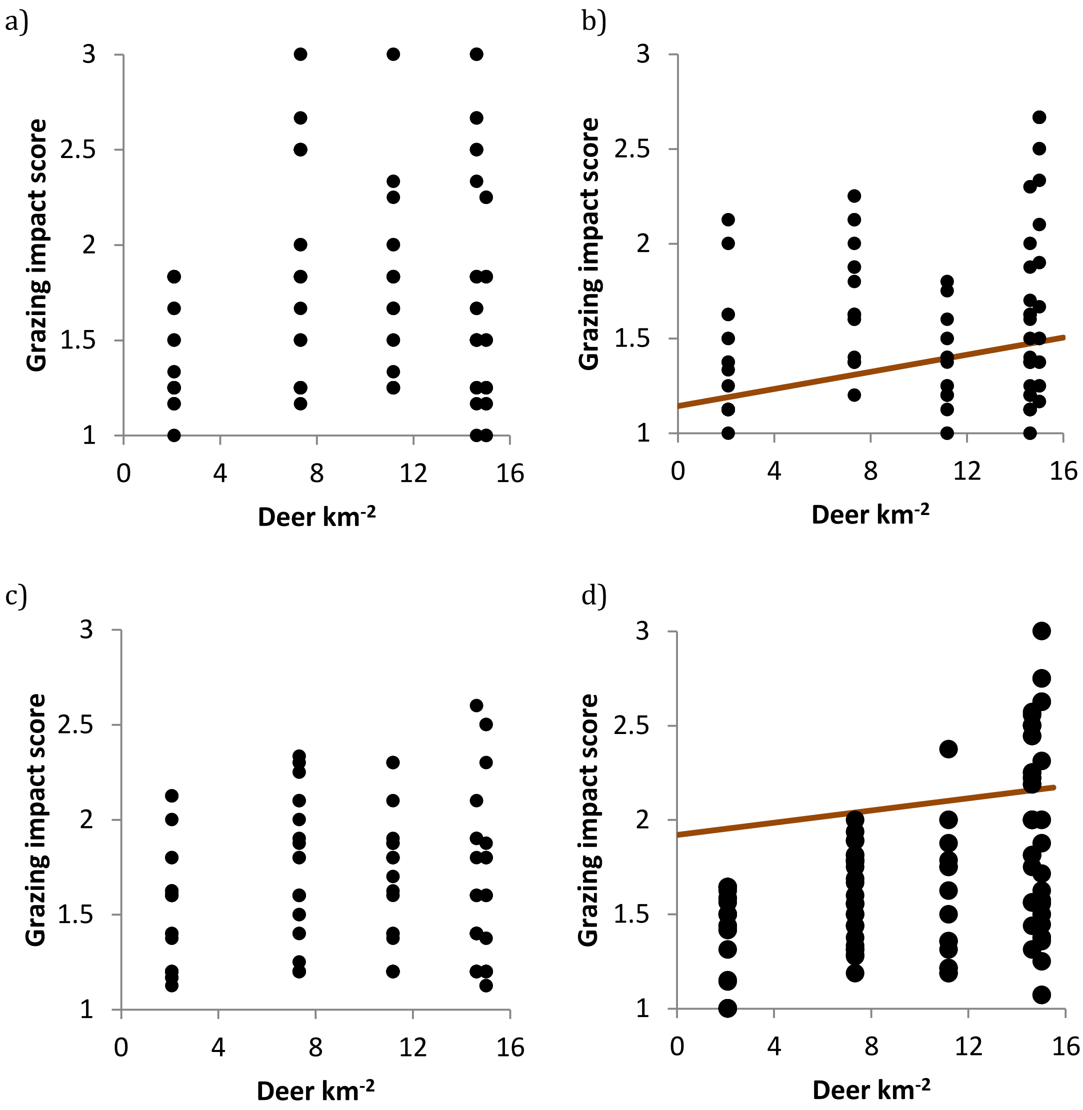

Fig 5.5: Fitted relationship between grazing impact score and Deer density, fitted lines shown only where Deer density is significant in the model. a) Blanket bog b) Dry Heath c) Wet heath; d) SRG.

5.5 Discussion

The hypothesis that an increased proportion of the preferred community in the surrounding landscape would increase grazing pressure was supported for all three less preferred communities (Blanket Bog, Dry Heath, Wet Heath), but was not supported for the preferred community, Species-Rich Grassland. I found support for the hypothesis that grazing intensity increased with increasing deer density for only two of the communities (Dry Heath and SRG).

Grazing management conflict

There was evidence of a conflict in managing for the conservation of both the attractive, grazing-dependent community (Species-Rich Grassland) and grazing-vulnerable Heaths and Blanket Bog. Roughly 20% of the less preferred communities were classed as overgrazed and 13% of the preferred community was classed as under-grazed over the whole study site. This survey was conducted in summer (August-September); summer is a critical period for SRG, as this is when there is maximum standing biomass and thus maximum light competition (Bento 2012). Low grazing in summer will allow vigorous grasses to become dominant, resulting in the lass of small herb species and an overall loss in conservation value of this community (MacDonald *et al.* 1998a). Grazing levels on heaths are likely to be higher in spring and late winter, as deer increase their use of evergreen dwarf shrubs over the autumn and winter periods, when grassland biomass is depleted and deciduous grasses have died off. So it is possible that the grazing patterns observed would change seasonally, although as grasslands are still selected for in winter (Charles *et al.* 1977, Gordon 1989b) some effect of the proportion of grassland in the local area is still likely.

Effect of proportion of preferred community within 1km on grazing impact

On the less preferred communities (Blanket Bog, Dry and Wet Heath) the results supported the hypothesis that grazing intensity would increase in areas where the proportion of preferred community was high. The effect size was fairly consistent, with 11-16% of the variance attributable to the proportion of grassland alone. The effect of the proportion of grassland was only significant when scales greater than 250 m away were considered. This indicated that resource quality was more important at the larger scales measured. Although this may have been partly due to the low variation in the proportion of grassland 0-250 m away from the less preferred communities. A previous study found that at a scale of 25 ha (similar in area to the 19.6 ha in the 0-250 m radius) the proportion of grassland present was positively correlated with *Calluna* utilisation on Dry Heath (Palmer *et al.* 2003). Increased grubbing on the less productive community in areas with an abundance of the productive was also found in a study of goose habitat use in the Arctic (Speed *et al.* 2009).

Contrary to my initial hypothesis, I found that where there was a large proportion of SRG communities were present within 1km, these communities were less heavily grazed. However, this effect only accounted for a maximum of 6.3% of the variance, and a proportion of this was confounded with the effect of deer density and block when these were included. An effect of the abundance of preferred community on grazing on the preferred community was found by Speed *et al.* (2009), but in that study the effect was increased use if the preferred resource where it was abundant, as would be predicted by marginal value theorem. So far as I am aware, there have been no other studies looking at the effect of the distribution of preferred food resource on the use of the same resource at spatial scales similar to that of the home range of the main herbivore using that resource.

Density relative to grassland resources was highly variable at the DMB scale and is likely highly variable at home range scales as well. The total area contained within the 1000 m radius is 314 ha, which is similar to the typical annual home range size of individual deer on the island and within the distance a deer can easily travel in a day (Lowe 1966, Pepin *et al.* 2004), it could be that a deer or group of deer with a lot of grassland in their home range distribute their impact more evenly over their range than those with a small area of grassland. Whereas where there is little grassland within the larger area, those areas act as intense focal points for grazing. Modelling suggests that herbivores are unlikely to conform to the ideal free distribution at scales greater than home range size (Tyler & Hargrove 1997). Since hinds remain hefted to a home range all their lives and daughters tend to remain in the same area as their mothers, deer density does not conform to the ideal free distribution at large scales (Fretwell & Lucas 1969, Conradt *et al.* 1999).

Differences between DMBs

The differences between deer management blocks on Dry Heath and Blanket Bog indicate that other unmeasured factors are important for explaining variation in grazing on these communities at this scale. Differences in topography, microclimate (particularly openness to prevail south-westerly airstream) and the contribution of other herbivores (which it was not possible to quantify in this study), are possible candidates. There is no consistent difference between communities in which DMB has the highest or lowest utilisation, so the contributing factors could be different between communities.

Effect of local deer density

Deer density was significantly correlated with increased grazing impact on only two communities but the variance explained solely by deer density was small in both cases. On Dry heath it explained 5.6% of the variance. On SRG effect of deer density was almost entirely confounded with the effect of elevation (23.2%) and the effect of grassland (2.1%), leaving only 1.6% solely attributable to deer density.

Previous studies have had mixed success in attributing differences in grazing impacts at small scales or the average impacts over larger scales to ungulate densities over several km^2: one study found that, on some communities, including some I assessed (Blanket Bog, and Heaths) red deer density was a good predictor of mean impact score across the community type in the Deer Management Group areas (which cover hundreds of km^2) The range of deer densities in that study was also slightly greater than in my study area (2.4 - 15 deer km^{-2} in 2008), being between 2.5 and 25 deer km^{-2} (Albon *et al.* 2007). Even so, they found no correlation between deer density and grazing impacts on some communities (Smooth grassland and Montane communities). A study on red deer browsing patterns found a correlation between deer density in the management unit and small scale browsing pattern on only one of three plant species (Mysterud *et al.* 2010). In a study addressing moose (*Alces alces*) browsing at multiple spatial scales, the correlation between dung counts and browsing became weaker as the scale increased (Månsson *et al.* 2007). It could be that the scale of the measurement was just too coarse to be meaningful for small scale impacts and smaller scale variation in deer density was more important and outweighed larger scale effects. As mentioned previously, it was unlikely that deer were distributed evenly with respect to food resources within a block (Ideal free distribution (Fretwell & Lucas 1969). Also the small number of deer management blocks means finding a correlation was unlikely if the effect size was not large.

Comparison with Chapter 4

There are several differences between indices of grazing used in this and the preceding chapter. *Calluna* utilisation measures the direct effect of browsing exclusively in one growing season. Sward height and litter depth are indirect measures, also affected by plant growth, senescence and decomposition rates. Insofar as sward height does represent grazing pressure, it will also include the effect of grazing in several preceding years; this is especially true of heaths, which are dominated by slow growing woody species.

Calluna utilisation proved to be a poor indicator for SRG and Alpine Heaths as there were many missing data points*.* On Wet and Dry Heath, missing data-points were not a problem, but there were few non-zero values in some years. Even at small (within plot) scales *Calluna* is likely to be selected against in the summer months, if there is grass present, as it is less digestible (Armstrong *et al.* 1997). An index based on a several species is less sensitive to small scale selection between species, which will be influenced by local species composition. This made *Calluna* utilisation a less appropriate measure for assessing the effect of large scale factors than the combined index, unless small scale species composition can be accounted for. *Calluna* would be a better indicator in winter, when it is used more as grasses stop growing and senesce, resulting in them becoming both less available and less digestible (Armstrong *et al.* 1997). It would also be an adequate indicator on heaths where it is the only dominant species, which is not the case in this study site, even Dry Heaths have a fairly variable composition and *Calluna* is not the dominant species at all sites. The major advantages of using an indicator comprised of data on impacts on several species is that some data should be collectable for every site and the index will be less influenced by selection within a site.

On the other hand, some of the data collected by the HIA method is qualitative rather than quantitative, and therefore can be subjective, and the semi-quantitative data that contributes to the index (e.g. proportion of grazed or browsed shoots on particular species) is divided into much broader categories. The grazing index is intermediate in terms of directness and the time period it records grazing for. The index includes some direct measures of browsing on specific plant species, or groups of species, on all plant communities. Some of the measurements will also reflect previous seasons' browsing; flowering can be influenced by herbivory in the previous year (e.g. Grant & Hunter 1966, Archer & Tieszen 1983) and in some species is influenced by weather conditions (e.g. Selas 2000, Bloor *et al.* 2010). Sward height and litter are included in the grazing index for SRG.

Despite these differences in the measurements, the direction and size of effects of proportion of grassland are broadly similar on Wet Heat and Dry Heath communities, which occur in both datasets. The effect of grassland accounts for 11-16% of variance in grazing impacts in this Chapter and 4 - 16% variation in sward height on Wet and Dry Heaths and up to 4.4% variation in *Calluna* on Dry Heath in the preceding chapter. Overall the effect of the proportion of grassland within 1km was strongest and most consisted between measures (grazing index, sward height and *Calluna* utilisation) on Dry Heath. The agreement between sward height and grazing impact index (and, on Dry Heath, *Calluna* utilisation), indicates that long term pattern of impacts (affecting sward height) are similar to short term impacts. And that the inclusion of elevation captured enough of the effect of micro-climatic variation on sward height that it did not obscure the proportion due to grazing.

The effect of deer density was generally small or negligible on the less preferred communities in both Chapter 4 and Chapter 5 results. Results for SRG are inconclusive, because of the confounding with elevation effect, but grazing index and *Calluna* utilisation are both positively correlated with deer density.

There are some differences: Chapter 4 found a positive effect of grassland area on two measures of grazing impact (sward height and litter depth) on SRG at small scales, as well as the negative effect of grassland within 500-1000m which was found for both sward height and the combined grazing index. However, browsing was increased on *Calluna* in the presence of more grassland at this scale. This indicates that the various measures of grazing impact on this community are not well correlated with each other. This could be due to a difference in the pattern of grazing on *Calluna* (which could be influenced more by small scale species composition affecting selection) and on other species or a difference between short-term summer grazing (measured by *Calluna*) compared to longer term average grazing patterns, reflected in sward height (as species composition will influence maximum height) and in some components of the grazing index.

Conclusions and management implications

Increased grazing of less preferred communities was found where there was a high proportion of the most productive community type that was most preferred by red deer at the scale of the study (up to 1km radius, which is 314 ha or 3.14km^2). Effects were largest and most consistent on Dry Heath. Increased grazing levels on less productive plant communities when there is a high proportion of a productive community present can be predicted from MVT (Charnov 1976). Increased utilisation of the less preferred community in areas with an abundance of the preferred one or in close proximity to the preferred one has been found in many studies at small scales (Clarke *et al.* 1995b, Dumont *et al.* 2002, Wang *et al.* 2009, Milligan & Koricheva 2013) . If has also been found in number of studies at larger scales, up to home range size of herbivores involved (Palmer *et al.* 2003, Månsson *et al.* 2007, Speed *et al.* 2009). Such an effect of increased grazing in proximity to an attractive resource is also commonly seen in foraging patterns centred on waterholes in arid rangelands, and around supplementary feeding stations in temperate and boreal forest (Pickup *et al.* 1998, Ball *et al.* 2000, Putman & Staines 2004, Mathisen *et al.* 2014).

Grazing impacts on the preferred resource was also apparently dependent on its local abundance; however, the effect size was smaller than, and in the opposite in direction from, the less preferred communities. This is contrary to the results of previous studies, which have generally found that the effect resource layout on use of the preferred resource (if there is an effect at all), is to decrease utilisation of the preferred resource in areas where the resource is less abundant at small (Barbosa *et al*. 2009, Wang *et al*. 2009) and large scales (Speed *et al*. 2009), which is in accordance with the predictions of MVT.

In the preceding Chapter (Chapter 4), the apparent effect of the proportion of grassland differs between different scales and different indices of grazing. The overall effect of grassland on utilisation of SRG is uncertain.

Deer density at the scale of several km^2 had little or no effect on grazing impacts on the less preferred communities. The results of Chapter 4 suggested that utilisation of SRG, at least when measured directly, was dependent on the local deer density, I was unable find firm evidence to support or refute the importance of deer density in this Chapter as the effect on the grazing index was confounded with elevation.

At these scales many factors affect animal habitat choice and therefore contribute to the variance in grazing pattern (Bailey *et al*. 1996, and see e.g. Månsson *et al*. 2007, Mysterud *et al*. 2010). The high proportion of unexplained variance in this study indicates that other factors are important such as topography, presence of other herbivores (which could not be quantified) and smaller scale vegetation pattern.

The consequence of increased utilisation of the less preferred communities in areas of the landscape where the preferred resource is abundant is that there where the communities in such a system are both of conservation concern, and the less preferred community is less tolerant of grazing there will be an inherent conflict in managing grazing levels for the benefit of both. It can be viewed as an example of association susceptibility, operating at large scale.

In this system, management conflict between preferred and less preferred communities will be highest in areas where the preferred resource is abundant. The effect size on the less preferred community, especially Dry Heath, is probably large enough that it is of some importance to management. Realistic management targets must account for the fact that ideal levels of grazing cannot be maintained on all areas of all communities simultaneously and should account for the effect, allowing for some compromise in condition of one community in order to benefit other in areas where a high proportion of the preferred community is present. Repeated monitoring of grazing impacts, preferably at fixed points, would determine whether the areas of over/under grazing were changing.

Chapter 6: Discussion and conclusions

6.1 : Exclusion vs reduction of grazing

Research question 1: What is the short term impact of reduction and exclusion of grazing on species-rich grasslands and how does this vary depending on initial conditions?

I found that excluding grazing led (within 3 years) to a severe decline in diversity and herb cover, changes that were detrimental to the conservation value of the grassland. The amount of change was dependent on biomass accumulated (and therefore on the productivity of the grassland, although accumulation of dead material will also be affected by exposure of the site), but the direction of change was the same across the range of grassland examined. Even a short period (three years) of grazing exclusion had dramatic effects on the grassland that would be hard to reverse. Longer term effects are likely to be continued loss of low-growing species due to increased dominance of competitive species present in the local area: *Festuca rubra* and *Calluna vulgaris* are the main candidate species at the study sites in Chapter 2. Others such as *Molinia, Ammophila arenaria* and *Arrhenatherum elatius,* although currently occurring only occasionally on the grassland, would be capable becoming important or dominant in the absence of grazing (Ball 1994, unpublished). Conversion to other community types such as tall herb or woodland would be limited by proximity to seed source. In areas far from a seed source, community change is likely to be to tall species poor grassland, grassy heath, or *Pteridium* dominated communities as bracken can spread rapidly and vegetatively and is a likely invader on grasslands on acid soils (Pearman, 2008). Tall herb communities are generally present only in fragmentary locations where inaccessibility to herbivores allows them to survive, thus seed sources are very limited and conversion of grassland to this type highly unlikely. Woodland species, mainly planted, are present in the main glens in lower lying areas, and elsewhere in very small fragments on steep slopes and stream banks inaccessible to herbivores (Pearman, 2008). It is possible that grassland in immediate proximity to such seed sources would convert to woodland or tall herb communities. The establishment of new species into newly established exclusion plots in proximity to a seed source would also depend on successful establishment in the limited time before the litter layer and grass canopy build up, as invasions after the canopy has built up are likely to be slow, taking many decades, if occurring at all. Even in Kilmory Glen, where there is a seed source present, the one remaining grassland exclosure of those studied by Ball (1972), now exceeding 50 years in age, contains only one stunted tree. No woodland species were recorded invading any of the plots in Chapter 2, although two birch seedlings were briefly present in Site 2 of the reduced grazing experiment.

Potential for recovery

Recovery from one season's removal of grazing was swift, but once species are lost, re-introduction of species after reintroduction of grazing would be slow except in the case of species which were able to persist in the seedbank. (In the small experimental plots, vegetative invasion form surrounding vegetation would likely restore species composition rapidly, but this would not be the case if exclusion was carried out over a much larger area). Reintroduction by endozoochorous dispersal would be a possibility as long as there was a donor site retaining these species within the range of the grazing herbivores.

Most studies of endozoochory rates find over 30% of species in the respective study areas (Malo & Suarez 1995, Mouissie *et al.* 2005, Iravani *et al.* 2011) are capable of being transported endozoochorously, and some studies report much higher levels, up to 75% (Mouissie *et al.* 2005). There has been less investigation of epizoochorous transport in fur (other than for sheep) or hoofs. However one study found transport in the hooves of bison to be an important dispersal vector in a mosaic of woodland, grassland and heath with a bias towards seeds that are long-lived in the soil seedbank (Schulze *et al.* 2014). Herbivore endozoochory has been shown to be an important process in maintaining the diversity of species rich subalpine and lowland grasslands (Iravani *et al.* 2011, Rosenthal *et al.* 2012). In the case of abandoned grassland (previously grazed), the (re)introduction of grazers can increase species diversity locally, and species not present in the abandoned grassland or its seedbank have been recorded to be introduced in this way (Traba *et al.* 2003).

Whether a plant species can be transported by deer (or other herbivore) between two sites is dependent on several variables: distance between sites; rate of consumption of seeds by herbivore; potential of seeds to survive gut passage; post dispersal seed predation; establishment of seedling at deposition site (Mouissie *et al.* 2005, Bruun & Poschlod 2006, Pakeman & Small 2009, Manzano *et al.* 2010).

Mean gut passage time of red deer has been recorded as between 27 and 41 hours (Milne *et al.* 1978). So long as the distance between source and potential deposition site is within the potential daily range of red deer, transport will not be limited by distance. Red deer are capable of traveling several km in a day (Drechsler 1991, Pepin *et al.* 2004). Home ranges on Rum are relatively small, usually extending up to a few hundred hectares (Clutton-Brock *et al.* 1982), transport of seeds between areas within a home range is likely along with less frequent longer distance transport by dispersing males. Rates of consumption of seeds by herbivores will depend upon the degree of selectivity of the herbivore and the abundance of the species in the vegetation. Thus preferred species, small-seeded plants where the herbivore is unable to select against the seedheads, species where seedheads are preferred, and more common species are more likely to be transported; conversely, the seeds of avoided or rare species are less frequently ingested (Bruun & Poschlod 2006, Iravani *et al.* 2011). Several studies find that smaller seeds appear to survive gut passage better, and so species with smaller seeds are often found to be more abundant in herbivore dung (Malo & Suarez 1995, Pakeman *et al.* 2002), although Bruun & Poschlod (2006) attributed this to a higher abundance of smaller seeds in the vegetation. Otherwise, the species composition of seeds present in dung appears to reflect a combination of seed supply in the vegetation and diet selection (Mouissie *et al.* 2005, Iravani *et al.* 2011).

The vascular plant species declining in the Chapter 2 experiments or becoming extinct in the older exclusion plots studies by Ball (1972; 1994 Unpublished) are listed in table 6.1 below. A brief review of the literature (search terms red deer and endozoochory) finds that of the 26 species for which records on the subject could be found, 16 appear to be able to survive endozoochory by deer in a viable form, recorded as germinating in greenhouse conditions. However, of these, eight were found not to germinate in all studies where the species was present. The other 10 species were not found to germinate from deer dung in any study although they were present in the vegetation or found in the dung of other species at the site.

Table 6.1: Species declining or locally driven to extinction in exclusion experiments on grasslands in Rum NNR from Chapter 2 plots and plots assessed by Ball (1972, 1994, Unpublished). Records of endozoochorous transport by deer and absence of transportation when known to be present in the vegetation summarised from literature records of deer endozoochory in habitats containing these species (grassland /heathland habitats) (Welch 1985, von Oheimb *et al.* 2005, Iravani *et al.* 2011). Germination was recorded in greenhouse conditions only and not in the field in the studies cited. Some species had viable seeds transported in some studies but not others.

Viable seeds present	**No viable seeds present**	**Viable seeds only sometimes present**
Antennaria dioica	*Anthoxanthum odoratum*	*Achillea millifolia*
Carex pilulifera	*Aira praecox*	*Cardamine flexuosa*
Cerastium fontanum	*Bellis perennis*	*Holcus lanatus*
Euphrasia officianalis (agg.)	*Botrychum lunaria*	*Lotus corniculatus*
Galium saxatile	*Carex panicea*	*Luzula campestris*
Luzula multiflora	*Carex pulicaris*	*Prunella vulgaris*
Plantago lanceolata	*Poa pratensis*	*Trifolium pratense*
Trifolium repens	*Rhinanthus minor*	*Veronica officianalis*
	Taraxacum officianalis	
	Veronica chamydris	

Species declining in exclusion plots but no data in searched literature: *Agrostis capillaris*;; *Carex arenaria*; *C. flacca*; *Cerastium vulgatum Cynosurus cristatus Danthonia decumbens*; *Galium verum*; *Gentianella campestris*; *Heiracium pilosella*; *Hypercium pulchrum*; *Hypochoeris radicata*; *Koeleria macrantha*; *Lathyrus montana*; *Leontodon automnalis*; *Oxalis acetosella*; *Parnassia palustris*; *Pedicularis sylvatica*; *Plantago coronopus*; *P. maritima*; *Polygala serpyfolia*; *Sedum anglicum; Senecio jacobaea*; *Thalictrum alpinum*; *Thymus polytrichus*; *Viola riviana*

Even amongst species readily transported, some may not establish in the field as readily as supposed from greenhouse germination studies: Red deer can transport tens of thousands of seeds in dung per day (Malo & Suarez 1995), however, seedling establishment from seed dispersed in dung may be low, and considerably lower than might be supposed from greenhouse germination of seedlings in dung (Welch 1985, Pakeman & Small 2009), due to field conditions that do not promote germination, or prevent seedling establishment (Welch 1985, Pakeman & Small 2009), or to post dispersal seed predation (Manzano *et al.* 2010). Where comparisons have been made between species, cattle appear to disperse many more species than deer (Welch 1985, Malo & Suarez 1995), and so introduction of cattle might encourage more long distance dispersal of locally extinct species. Introducing multiple species of grazers would almost certainly increase the number of species transported (Welch 1985, Schmidt *et al.* 2004, Eycott *et al.* 2007). Additional species would potentially be transported in hooves or on animal fur, even when lacking adaptations to ectozoochorous transport such as burs and hooks on seeds (Schmidt *et al.* 2004, Schulze *et al.* 2014).

In summary, data on potential transport of specific species is limited, but reintroduction of species by endozoochory is a probable mechanism for some of the species that are outcompeted on these grasslands following grazing exclusion. However, other species do not appear to be transported by deer. Reestablishment from this source might be slow even for easily transported species, taking many years, due to low rates of establishment following endozoochory.

Reduction of grazing

Experimental reduction of grazing by large herbivores is more difficult and costly to implement than total exclusion. However, a reduction of grazing intensity (to between 20 and 70% of the control plots) was achieved and the resultant changes on reduced grazing plots were much slower, as would be expected. Species cover changed little in response to reduction of grazing, with little general trend evident after 2 ½ years compared to significant shifts in composition after only one growing season in exclusion plots (Chapter 3). There were some effects on cover of common species and broad functional groups, but these changes were also dependent on starting sward height. When compared to conservation targets for the grasslands, some plots were initially apparently over-grazed, the main indicator for this being that the sward was shorter than target height, while other plots were under-grazed (taller than target height). The effect of reducing grazing in terms of fit to the same targets differed depending on starting conditions. On sites that initially had very short swards, reduction of grazing improved the fit to sward height targets, whilst plots that fit the criteria, or were already too tall, moved further from the target height.

This highlights a problem with applying the criterion of a specific height structure at a set spatial scale on grasslands with diverse species composition and productivity. Large herbivores grazing on swards that are more nutrient-rich when kept at a younger growth stage by repeated grazing will return to grazed patches, resulting in the development of a sward containing very short grazing lawns and contrasting taller, rarely grazed patches (Cid & Brizuela 1998, Beecham *et al.* 1999). The scale of heterogeneity that develops in such a sward is hard to control as it has been found to vary depending on many factors including initial vegetation pattern, scale and strength of herbivore selectivity productivity and timing of measurement in relation to period of growing season (Adler *et al.* 2001, Rossignol *et al.* 2011, Dumont *et al.* 2012). In the case of the Rum grasslands, the target sward structure called for fine scale heterogeneity in height (at the scale of 1 m^2), but, with the exception of areas that contained many tussocks, sward heterogeneity appears mainly at a larger scale on these grasslands (tens to hundreds of m^2).

The diversity of grassland conditions over a small area (differences in utilisation levels and productivity) makes extrapolation from small scale experimental plots challenging. Overall, the results of the exclusion experiment and the reduced grazing experiment highlight that heterogeneity in starting conditions will affect the rate of response to changes in grazing regime and the effect changing grazing regime will have on meeting conservation targets. Due to the large-scale spatial pattern of grazing with the grassland area, there may be a trade-off in managing to reduce overgrazing on heath and on some areas of grassland, at the expense of allowing other grassland areas to become under-grazed. Grazing with cattle is one management option that might even out grazing at this scale on the grasslands but cattle, being less selective grazers are also likely to even out small scale heterogeneity in sward height. Cattle graze heath much less frequently than deer do, so replacement of some of the deer grazing pressure with cattle could benefit heath without penalising grassland.

The slow response to reducing grazing compared to grazing exclusion makes predicting long-term consequences of changes to grazing regime from short-term experiments difficult if not impossible. Long-term experiments imposing different grazing levels over reasonably large areas are expensive to run however (Marriott *et al.* 2004), and small scale but long term studies might fill in some gaps in our knowledge. The method of semi-permeable fencing proposed and tested (Chapter 3a), was found to be successful in reducing grazing and represents an alternative method of implementing long-term experimental grazing reduction that is cheaper than a large-scale study.

6.2 Influence of large scale spatial pattern of vegetation on grazing impacts

Research question 2: To what extent can the distribution of plant communities at the landscape scale (100s m^2 to km^2) explain small scale grazing impacts on preferred and less preferred communities? How does this interact with deer density?

I found that grazing impacts on both the preferred and less preferred communities in a complex mosaic were affected by the spatial layout of communities at scales of 100-1000s m^2. These results are in agreement with the findings of earlier studies suggesting that the spatial pattern of grazing on the less preferred community is affected by the spatial layout of vegetation communities at similar scales (Palmer *et al.* 2003, Speed *et al.* 2009). The effect on grazing impacts on the preferred community was somewhat weaker than the effect on the less preferred community, furthermore, the direction of the effect (increased or decreased grazing in areas with a lot of grassland) varied depending on scale and measure of grazing used. Further studies are needed to determine the whether this relationship is biologically important. The effect on the preferred community has less often been addressed at large scales, but one other study found that use of the preferred community was increased in areas where there was a high proportion of preferred community at scales of 100s m^2 (Speed *et al.* 2009).

Differences between the two datasets

In comparison to an index of sward height (Chapter 4), the grazing impact index used in Habitat Impact Assessments (Chapter 5) uses mainly direct indicators of browsing or grazing, although sward height is one of several measures used for grassland communities. The use of multiple indicators in an index ensures at least some data can be collected for each site. A drawback of the index compared to more quantitative measures is that the categories of impact for individual indicators are quite coarse and in some cases indicator assessment can be subjective. However a recent study found that although small differences between surveyors in assessment of overall status and individual indicators was common, radical disagreement was rare (MacDonald 2010).

Sward height and litter measurements in the Chapter 4 dataset are quantitative and more precisely measured, leaving less room for subjectivity. However, they are indirect indicators of grazing as they are also strongly dependent on productivity, senescence and decomposition, and maximum potential sward height is also dependent on species composition. The time period over which sward heights represent grazing impacts is uncertain; especially in communities dominated by dwarf shrubs, sward height will be the product of grazing and productivity over a number of previous years as well as being affected by recent grazing. On grassland, sward heights will respond more rapidly to changes in grazing and should mostly represent the balance between productivity and grazing in that year. However, grazing-induced changes in species composition can in the longer term affect the sward height, and in particular this can control potential maximum sward height. Since sward height affects the competition environment experienced by the plants, changes in height will have an effect on future species composition changes, so sward height is useful on all communities to have as an indicator of the likely effect of grazing on the community.

On the other hand, *Calluna* utilisation, as used in Chapter 4, is a direct measurement of browsing occurring in the year of measurement, as the annual growth pattern of heather means that the current year's grazing can be separated from lingering evidence of grazing in previous years (Mohamed & Gimingham 1970). *Calluna* utilisation was less useful as an indicator on species-rich grassland and Alpine Heath, as the species was not present or was present in very low proportion in many plots, resulting in missing data for 30-35% of plots, or values based on measurements of very few *Calluna* shoots. This was not such a problem on Wet and Dry Heath, where *Calluna* was often abundant or dominant and was at least present in all plots except for 4.6% of Wet Heath plots (Britton & Pakeman 2009).

Effect of plant community distribution on grazing of less preferred communities

There is agreement between the analyses in Chapter 4 and that in Chapter 5 that spatial vegetation layout at the scale of 100s – 1000s of m^2 is important to patterns of grazing impact on the less preferred communities. All correlations between the area of grassland within 1km and grazing indicators on three of the four less preferred communities (Blanket Bog, Wet Heath, Dry Heath) showed increased grazing impact where there was more grassland in the immediate area, at scales of 250 - 1000 m. The effect was consistent in direction and broadly consistent in strength (4-18% of variance in grazing impact explained where significant) across communities. The correlation was found between sward height and area of preferred grassland within 1km and grazing impact index and preferred grassland within 1km, for all communities. However, *Calluna* utilisation was only correlated with adjacent grassland area on Dry Heath. This can be considered an example of associational susceptibility. In large herbivore foraging studies this effect has frequently been found at small scales: in a grass-dry heath community mosaic (Hester & Baillie 1998), on artificial grass swards (Dumont *et al*. 2002), and in patterns of browsing by large herbivores feeding in forests or in stands of trees (Barbosa *et al*. 2009).

Because of the different model types used in Chapters 4 and 5 (linear mixed versus linear models) the R^2 measurements from these different models, although analogous, are not precisely comparable (Liu *et al*. 2008). However, of the three communities that appear in both datasets (Dry Heath, Wet Heat, SRG) Dry Heath had the highest degree of variance attributable to the proportion of grassland within 1km in both datasets, and the correlation with grassland is consistently present across all grazing indicators (except that in 2008, *Calluna* utilisation was zero on most plots, so no correlation was found for this year). This is possibly because, amongst the less preferred communities, it is selected for more often: some studies have found a greater degree of selection for Dry Heath compared to Wet Heaths or Bogs (Gordon 1989b, Milner *et al.* 2002) (although still much less than selection for grassland). However, this is not a ubiquitous finding, one study of habitat preference found that red deer had a roughly equal avoidance of Dry Heaths compared to Wet Heath and Bogs throughout the year (Charles *et al*. 1977).

The commonality of the effect of the area of grassland in the locality on sward height (which in dwarf-shrub dominated communities will reflect grazing in several previous years) and the more direct measures of recent browsing contributing to the grazing impact index and *Calluna* utilisation in 2001 and 2003, suggests that influences on the pattern of grazing have been broadly consistent across years. (The difference between years in the spatial pattern of *Calluna* utilisation on Dry Heath found in Chapter 4 was due to very little browsing being recorded anywhere in 2007).

Effect of plant community distribution on grazing of the preferred community

At the smallest scale investigated (250 m radius), I found an increase in utilisation of species-rich grassland (SRG) where there was a high proportion of grassland in the vicinity, but this was only found for sward height and litter depth (Chapter 4) and was not found to affect *Calluna* utilisation or the combined index of grazing impact (Chapters 4 & 5). However, at the largest scale (500 -1000 m) there was a negative correlation found between proportion of grassland within 1km and sward height and grazing index. There was no correlation between grassland at this larger scale and litter depth. The variance explained by grassland at this scale is between 3 and 9% for sward height and grazing index, similar to the variance in utilisation on other communities that is explained by area of preferred grassland within 1km (see above). There was however, a positive correlation between *Calluna* utilisation and area of preferred grassland at this scale (although variance explained was only 3.7%), contradicting the impression gained from the sward height that grazing decreases with less preferred grassland present at this scale. This indicates that there is a difference in apparent utilisation depending on the measurement used for this community. *Calluna* utilisation on species-rich grassland is likely to be highly dependent on local species composition, as it was generally present in low abundance and would be selected against at a small scale, and so on its own is probably not a good indicator of overall grassland utilisation.

There was a reduction in the strength of the relationship between grassland sward height and proportion of grassland within 500 - 1000 m in 2008 compared to 2001, 2002 and 2003 (Chapter 4). A relationship between grazing impact on species-rich grassland and the proportion of preferred grassland at this scale is nonetheless detectable in the combined grazing impact index collected in the same year (Chapter 5). Sward height is dependent on productivity as well as grazing, whereas the grazing impact index includes more direct measurements of recent grazing, so the difference in results for sward height between years could reflect inter-annual differences in productivity, rather than differences in grazing patterns.

Spatial layout of different food sources or vegetation types has been found to cause variation in consumption of the preferred food resource at various scales (Barbosa *et al.* 2009, Speed *et al.* 2009, Wang *et al.* 2009). Associational resistance is the opposing effect to associational susceptibility (discussed above) and describes the situation where the preferred resource is used less where there is a low proportion of the preferred resource (and consequently a high proportion of the less preferred food resource). Such an effect is commonly found in patterns of ungulate browsing on individual trees in forests and has also been found for deer grazing on open habitats at the scale of individual plants (Barbosa *et al.* 2009, Bee *et al.* 2009). Likewise, a study on geese grazing on open habitats found an increase in use of a preferred community where there was more of it within 500 m (Speed *et al.* 2009).

Associational resistance was found when considering the smallest scale (0 - 250 m), perhaps because this scale is much smaller than home range size (Clutton-Brock *et al.* 1982), and within the home range there is greater selection for areas that contain larger patches of preferred grassland or a greater number of small patches of grassland. Both of these scenarios lead to decreased travelling costs between feeding sites.

The mechanism behind the negative correlation between area of preferred grassland and utilisation of SRG – as indicated by sward height (Chapter 4) and grazing index (Chapter 5) – at the larger scale is not obvious. However, since the larger spatial scale is close to (or slightly larger than) average deer home range size on Rum (Lowe 1966, Clutton-Brock *et al.* 1982), it is possible that the negative correlation between grazing on species-rich grassland and the area of preferred grassland within 500-1000 m emerges from the following: deer with home ranges containing little grassland would focus their grazing on these small areas, in contrast to deer with home ranges containing a larger proportion of grassland who would disperse grazing more evenly within the home range. Owing to its apparent complexity, the relationship between the spatial layout of plant communities and grazing on the preferred community merits further investigation.

Effect of deer density on grazing impacts

In general, deer density at the scale measured was found to be a poor predictor of impacts for any indicator. In most cases, the influence of the area of preferred community was greater.

Deer density and deer km^{-2} preferred grassland were correlated with grazing index (Chapter 5) on only two communities (Dry Heath and SRG); in the Chapter 4 dataset, correlations were found with sward height and/or *Calluna* utilisation on all communities, but some of the correlations were in a counterintuitive direction (higher densities correlated with less grazing impact). There was also no consistency in which of the measurements (deer km^{-2} or deer km^{-2} preferred grassland) was significant or was the better fit, when either one was significant in the model. The variance explained was either small (<4%) or largely confounded with other variables. There was one exception to this: the positive correlation between deer km^{-2} preferred grassland and *Calluna* utilisation on *Nardus* grassland explained ~13% of the variance. The interaction between grassland area and deer density was tested for (where main effects were significant and sensible i.e. in the direction of more deer predicting increased impact) but again found statistically significant interactions produced results which could not be interpreted, i.e. decreasing impacts with increased deer density, within the range of deer densities that were present, and the additional variance explained by including the interaction was in all cases small.

The small number of areas for which deer density information was available and the lack of hard boundaries between them perhaps meant that finding correlations on this scale was unlikely. Since the differences in density over time and across blocks were small (typically a twofold difference between blocks within the same year, with the exception of DMB 5 which had exceptionally low numbers and densities of deer) it is also possible that the magnitude of differences was too small to make a noticeable difference at the scale studied. However, deer km^{-2} of preferred grassland had a much larger range in magnitude (in 2008 there was a range of 84-452 deer km^{-2} preferred grassland), and still there was no consistent pattern of impacts in relation to this measure. It is not uncommon for density of large herbivores at larger than home-range scales to have little apparent relationship to local grazing or browsing impacts, or to be related to grazing or browsing on only some of the plant communities and species studied (Albon *et al.* 2007, Månsson *et al.* 2007, Mysterud *et al.* 2010)

There were however, differences between Deer Management Blocks found for several communities (SRG, Blanket Bog, Dry Heath, and Alpine Heath) in both datasets (Chapter 4 & 5). Deer Management Block appeared to be particularly important for SRG, with DMB being a significant factor for all measurements of grazing impact analysed in Chapters 4 & 5, and explaining up to 22% variance. DMB was a better explanatory variable than deer density or deer km^{-2} preferred grassland for grazing impact index, being significant in the models more often, despite using additional degrees of freedom. In the case of grazing index on Dry Heath and Blanket Bog (Chapter 5) it explained a higher proportion of variance than deer density.

This points to some other variable(s) differing at this scale that has not been taken into account. However, differences between blocks were not consistent between communities or between different grazing impact measures on the same community, so it was not possible to attribute the differences to any particular factor (e.g. the presences of some other herbivores in some blocks).

6.3 : Implications and recommendations for management

Research question 3: What are the implications of the effect of grazing reduction or exclusion on species-rich grassland (question 1), and the effect of spatial pattern of vegetation on distribution of grazing impacts (question 2) for conservation management?

The main outcome of this thesis has been to highlight the importance of taking the spatial pattern of grazing into consideration when setting management goals for a multi-community mosaic and implementing a grazing regime to satisfy these goals.

Grasslands

I found that the consequences for grasslands of being under-grazed can rapidly become severe, including species loss, something it would be hard to recover from if species were lost over a large area. Reintroduction of propagules by grazing herbivores once grazing was resumed would be possible, as long as the species lost from the grassland with grazing exclusion were still present in other areas of grassland and able to survive endozoochory, or are able to transfer by external attachment to herbivores. As discussed in section 6.1, there are a number of species for which endozoochory does not appear to be a likely route. Temporary exclusion of herbivores, for example to promote recovery of heath, is therefore not an appropriate measure where the interspersed grassland is also of conservation importance. Additionally, in areas of degraded heath where grasses have become dominant, total exclusion of grazing may not achieve reestablishment of dwarf-shrubs, in any case (Mitchell *et al.* 2008).

Spatial heterogeneity of grazing within grassland can make it difficult to design management that will enable conservation targets to be fulfilled in all areas (see Chapter 3b). On Rum, polarisation of grazing intensities between heavily used lawns and less used areas meant that few areas would fit the current standards for appropriate grazing levels, some failing for being under-grazed and some for being overgrazed, an earlier survey found the same pattern (Dayton 2011). Reduction of grazing pressure, although not as rapidly detrimental to grassland as exclusion, would likely not change this polarised pattern. There are methods (usually applied to domestic stock) which encourage homogeneity of grazing, such as stock rotation, herding and placing attractive resources (e.g. mineral blocks or supplementary feed) in under-utilised areas (Bailey *et al.* 1998, Ganskopp 2001). Some of these methods would be practicable with wild herbivores. However, supplementary feeding can cause problems in itself, by concentrating impact intensely in one area, and dependence on supplementary feed can be detrimental to animal condition (Schmidt & Hoi 1999, Putman & Staines 2004, van Beest *et al.* 2010a). In many situations, supplementary feeding is not generally desirable due to loss of the aesthetic 'wildness' and the general detrimental effect of import of nutrients on unimproved, species-rich grassland and other semi-natural plant communities (Bokdam & Wallis De Vries 1992, Janssens *et al.* 1998, Bokdam 2001, Hartley & Mitchell 2005). Additionally, if levels of supplementary feed are sufficiently high, it can allow the herbivore population to increase above the carrying capacity of the vegetation, resulting in very high impacts on the vegetation (Putman & Staines 2004).

Mixed-species grazing might also be an option to even out the effects of grazing: larger species generally need taller swards to maintain their intake than smaller species, and in a mixed grazing system, competitive exclusion will result in their making more use of taller swards in periods of food shortage (Illius & Gordon 1987). In the system described, cattle are an ideal candidate: cattle need taller swards than deer or sheep to maintain an adequate intake rate, so the introduction of cattle to an area under deer or sheep grazing could be used as a tool to increase grazing offtake on the taller grassland areas. Cattle grazing has been found to facilitate grazing by deer on Rum (Gordon 1988), and in other places (Kuiters *et al.* 2005). Swards previously grazed by cattle are used more by deer later in the season than those that are not (Gordon 1988, Kuiters *et al.* 2005). This would likely at least result in the spread of species rich *Nardus* grassland to closer to its maximum potential area (species-rich grasslands are restricted to the better drained soils on Rum and do not occur on peat). However the introduction of cattle would need to be coupled with deer control so as not to increase the total grazing pressure on the area

However, and importantly, it is not to be assumed that changing the scale of heterogeneity to align with SCM targets (reducing heterogeneity of grazing at scales >1m, and increasing small scale (1m^2) heterogeneity), would be of net conservation benefit. This has already been discussed at more length in Chapter 3b, but to summarise: SCM targets only focus on the plant community and do not take into account the needs of other species groups. The current large scale variation in grazing levels on grasslands is probably beneficial for invertebrate diversity compared to a more uniform sward that would be promoted by SCM targets (Dennis *et al.* 2002, Dennis 2003) and plant species diversity could be supported by large scale rather than small scale heterogeneity in the sward. The target for heterogeneity at 1m^2 scale is impractical, as heterogeneity at such fine scales is largely outside of management control, or rather, as it is dependent on so many underling factors, its response to management changes is unpredictable (Scimone *et al.* 2007, Dumont *et al.* 2012) (see Chapter 3b).

Managing mosaics

In a multi-community mosaic, where more than one community is of conservation value, and they require different levels of grazing to preserve their value, problems may arise when trying to manage for all of them. It is common for designated conservation areas, especially larger sites, to have more than one community that is of conservation value (McLeod *et al.* 2009), yet conservation goals are often set on a per-community basis: this might be unrealistic where communities are present in mosaic. Where grazers are allowed to roam freely, the level of grazing each plant community receives depends on their relative attractiveness to the herbivores and their relative accessibility. If the more grazing-vulnerable community is also the community preferred by herbivores, there is a clear choice in managing for one community or another: an attractive, grazing-vulnerable community will only persist in inaccessible areas (unless otherwise protected by fencing the plant community or herding animals), or if grazer numbers are lowered to levels that are is likely to be incompatible with managing other communities that require grazing. However, in the case that the preferred communities also need higher grazing levels or are robust to higher grazing levels, the probability of conflict is lower.

Such a situation is present in a mosaic of species-rich grassland and heath and bog communities: the species-rich grassland needs grazing to maintain diversity (Halada *et al.* 2011, Hejcman *et al.* 2013), whereas the heath and bog communities are sensitive to excessive grazing and trampling (Milne *et al.* 1998); grassland is also the preferred community, being dominated by more easily digestible species (grasses rather than dwarf shrubs) (Armstrong *et al.* 1997). It is therefore possible to imagine a scenario where grazing levels can be maintained within acceptable limits without fencing or herding. However, conflict may still arise as grazing will not be spatially uniform within a plant community.

I found that grazing was increased on less preferred communities (Heaths and Blanket Bog) in areas with a high proportion of grassland at large scales (up to 1km radius); this will increase the potential for conflict in management in areas where there is a high proportion of the preferred community. In the context of UK upland communities, Dry Heath appeared to be more affected by this than wetter communities. The decrease in grazing on grassland where there was much grassland within the wider area (500-1000 m) could further increase conflict in areas where there is a lot of grassland present, as it implies that there will be less difference in the grazing intensities between grassland and the less productive communities in such areas. Therefore heaths are more likely to be overgrazed and grasslands more likely to be under-grazed in such areas. Conversely, in areas with little grassland, there will be less conflict: grassland is apparently grazed more and heaths less in such areas.

However, the effect on the grassland community was relatively small and not as consistent between years as the effect on heath, implying some interaction with productivity and/or deer density. This is an area that would benefit from further investigation before strong general conclusions can be drawn about the importance of community spatial layout for grazing on the preferred community.

Using different species of herbivores, where practicable, may have the potential to decrease conflict between grazing of adjacent communities, although it is unlikely to eliminate it; e.g. sheep and cattle use heather less than deer and combined deer and sheep grazing on grass-heather mosaics has been found to decrease the impact on heather compared to deer alone, on the other hand, sheep have more intense local impacts, which may be undesirable (Hope *et al.* 1996, DeGabriel *et al.* 2011).

Setting management goals and possible management options

Management goals need to be very clear and must include recognition that grazing impacts are not spatially uniform, either at small (10s-100s m^2) or large (1km–10s km^2) scales. Where conflict is present, management goals need to either explicitly prioritise one type of habitat or allow for compromise of some areas of one community to benefit other communities.

The uncritical use of targets for the conservation status of plant communities based on standards set at a national or international level can lead to unwarranted criticism of site management for failures to meet community criteria when there is inherent conflict in management and it is likely impossible to maintain the required area of all community types in favourable condition. Identifying such conflict as the cause (or likely cause) of condition failures would allow more realistic and site-specific goals for community condition to be set. In practice this is likely to mean prioritising management for one community over another or allowing a proportion of the vulnerable habitat to fail, if it is in close proximity to a community that requires more grazing.

Sacrificial area(s) of vulnerable community might be identified, as recommended in Chapter 4 and 5, where overgrazing of these communities is allowed in order to benefit an adjacent grazing-dependent community. Over a large site (100s km^2), culling or other herbivore management could be used to establish different densities in different areas to benefit different communities. For example, maintaining higher densities in areas where there is a lot of the preferred community and it would in any case be difficult to avoid detrimental impacts on the more vulnerable community without compromising the more productive community, whilst lowering herbivore densities in other areas to promote the conservation of the community less tolerant of grazing at the possible expense of the productive, grazing-dependent community. Maintaining different densities has been shown to be possible on Rum, over the relatively small area of the DMBs (14-25 km^2) (Clutton-Brock *et al.* 2002a, Clutton-Brock *et al.* 2002b), although in areas where deer range more widely and the topography is less restrictive, the minimum scale over which establishing different densities is possible is likely to be larger. However, continual effort would be required to maintain such differences against migration from other areas. Differences in density are also more likely to show a correlation with impacts on less preferred compared to preferred communities (Albon *et al.* 2007). Differences in density might have limited effect, unless the differences were very large; it is important to note that although average grazing levels would likely be lowered, smaller scale spatial patterns, such as increased grazing impact in proximity to the preferred community, would persist.

Given the complexity of factors affecting spatial distribution of grazing impact, a pragmatic approach might be repeated monitoring in the same location rather than attempting to determine *a priori* which areas are likely to see high/low impact. Repeated monitoring at a network of fixed points would be recommended to test whether the effects of grazing were spreading or becoming unacceptably high.

For Rum, if the focus is maintained on the plant communities, there would be an argument to focus on the grasslands on the basis that they are the rarer habitat on Rum being more restricted to the better drained, more base-rich and neutral soils, which are rarer on Rum than the acid peaty soils on which heaths thrive (Pearman *et al.* 2002). Species-rich *Nardus* grassland is also less common at a UK scale compared to the heath types present on Rum and has fewer protected sites (JNCC 2012 b, c, d). Maintaining plant diversity on species-rich *Nardus* grassland could be achieved at least cost to other habitats by reducing goat numbers, and allowing other herbivore numbers to increase, as goats make more use of heath communities than the other herbivores present (Gordon 1989b). Replacement of some deer with cattle would be possible in lowland areas, which would again reduce the impact on heath. However, cattle grazing would be impractical for higher elevation grasslands on steep ground, and these appear to be the least grazed, according to HIA. Reducing deer numbers would therefore increase the problem of undergrazing on these grasslands. Undergrazing in these grasslands may be an unavoidable problem, even with this community prioritised: in the south Cuillin, there are areas of coastal grassland overgrazed (the only overgrazed grassland on the island) <1km distant, but at elevations of <600 m there are grasslands recorded as undergrazed (see Fig 6.1). However, although higher elevation plots in the Cuillins were amongst those least grazed according to the HIA index (Chapter 5; Fig 6.1) which measures mainly direct indications of grazing, there was only a small effect of elevation on sward height: lower tussock height at higher elevations (Chapter 4). This suggests that climatic restriction on sward height is maintaining shorter sward heights on higher elevation grassland and thus low grazing levels are less likely to result in loss of low-growing species than in lowland areas. Certainly the areas of grassland lost between 1960s and late 1990s (see Section 1.3 and Appendix 1), are mainly at lower elevations (Ferreira 1970, Bates *et al.* 2002).

I would also advocate some review of the guidelines used to assess grassland condition, especially the restrictive height guidelines. As outlined in the previous section and in Chapter 3b, the guidelines for sward structure may not be achievable on some grasslands and larger scale variation in sward heights could probably supply the same range of niches for plant species (see section 3.9).

Implications for other taxa

Consideration of other taxa that use the grasslands could lead to different conclusions about the level of grazing that would maximum conservation benefit on grassland. Although thorough consideration of the implications of particular grazing regimes for other taxa is beyond the scope of this thesis, a brief discussion of the current state of knowledge seems merited as there are numerous species of conservation concern in other taxa present on Rum (SNH 2009). Over 2500 species of invertebrate have been recorded from the island, these include 62 nationally scare invertebrate species, including 15 Red Data book species (SNH 2009), some of which are associated with grassland[1] (e.g. *Hepialus humuli*, *Scotopteryx chenopodiata*, *Bombus muscorum*) Wormell 1982, SNH 2009). Around 90 species of bird are recorded as breeding on the island, including 15 priority conservation species (SNH 2009). Numerous passerine and wader species that make use of moorland and grassland habitats for nesting and foraging have breeding populations on Rum, including several species of international conservation concern (SNH 2009). Bird and invertebrate assemblages can be profoundly affected by grazing management decisions (Tscharntke & Greiler 1995, Fuller & Gough 1999).

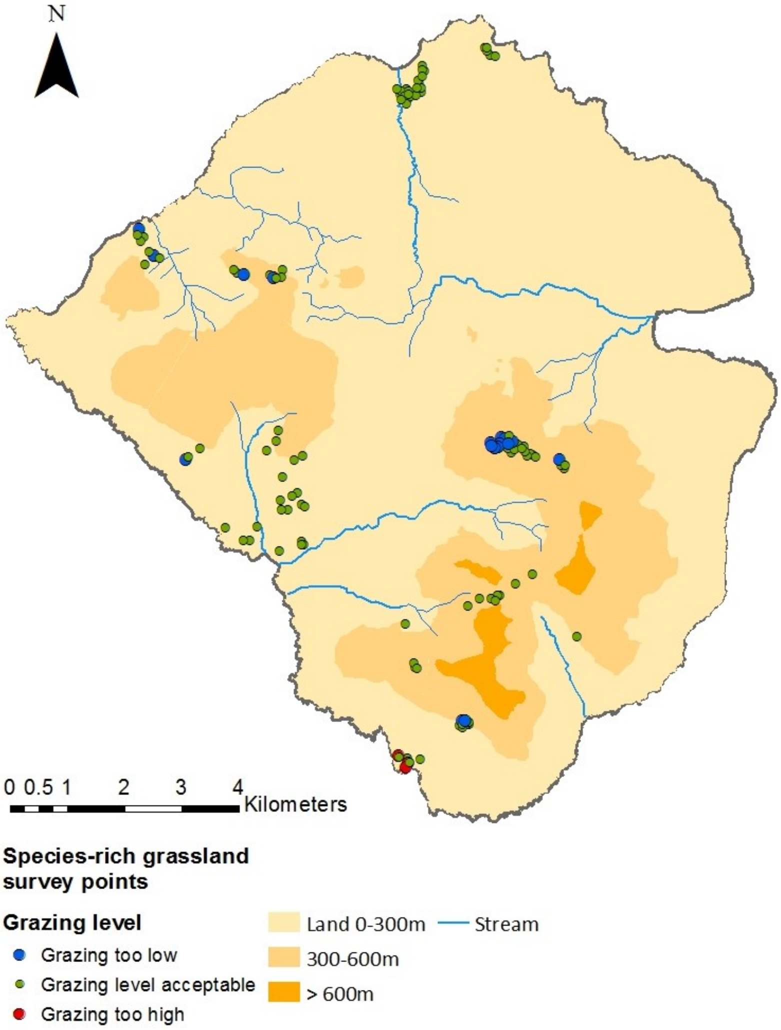

Fig 6.1: HIA plots on species rich grassland showing category of grazing (low, acceptable, high). See Table 5.1 for comparison of these categories to numeric scale of impacts.

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[1] The highest diversity of invertebrates (including some of these protected species) is associated with woodland (Wormell 1982) and encouraging these species by encouraging spread of woodland would necessarily result in loss of open habitat and require radically different management to encourage woodland regeneration.

A diversity of invertebrates and bird species is frequently encouraged by extensive grazing and some variation in grazing levels is often recommended to encourage a greater number of species across a site as a whole; this may sometimes be compatible with the recommended range of grazing intensity for plant communities (Dennis *et al.* 2002, Buchanan *et al* 2006, Pearce-Higgins & Grant 2006, Dennis *et al.* 2008). However, for particular plant-animal communities and species there will be some degree of conflict. Grazing recommendations for insect diversity are for lower grazing levels than for maximisation of plant diversity on lowland calcareous grassland (where this has been well studied) (Wallis De Vries *et al.* 2002, van Teeffelen *et al.* 2008). Tall and structurally diverse swards also tend to promote invertebrate diversity on upland grassland with some species thriving in ungrazed swards (Dennis *et al.* 1998, Dennis 2003). However there are also specialists of heavily grazed swards that benefit from areas of heavily grazed swards, including priority conservation species (Morris 2000, Pöyry *et al.* 2006, Davies *et al.* 2007). Floristic diversity (which is encouraged by a short sward) has also been found to be positively correlated with diversity of herbivorous invertebrates (Tscharntke & Greiler 1995, Woodcock & Pywell 2010).

Birds associated with upland habitat mosaics of moorland and grassland are affected by grazing through both habitat availability structure and through the availability of invertebrates as a food source (Fuller 1996, Fuller & Gough 1999, Buchanan *et al* 2006, Pearce-Higgins & Grant 2006). As with invertebrates, although some species need lightly grazed, taller or tussock-containing swards for nesting (e.g. Snipe *Gallinago gallinago*), others make use of both tall, lightly grazed vegetation and shorter swards (e.g. Curlew, *Numenius arquata*), often relying on taller swards for concealment and short swards for feeding; and a few species are associated with heavily grazed swards (e.g. Wheatear *Oenanthe oenanthe* , Golden plover *Pluvialis apricaria*) (Fuller 1996, Fuller & Gough 1999, Pearce-Higgins & Grant 2006)[2]. A focus on bird or invertebrate taxa would therefore lead to the recommendation of more varied, and probably overall lighter, grazing on grassland than a focus on plant diversity (Fuller 1996, Pearce-Higgins & Grant 2006; Buchanan *et al* 2006).

The current polarisation of sward heights recorded on some grasslands on Rum, although not in line with recommendations for the plant community, might therefore be beneficial to maintaining a diversity of bird and invertebrate populations.

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[2] The examples given are all species that are recorded to breed on Rum (Anonymous, SNH 2009).

Generality of results

The main plant communities of the Isle of Rum (heaths and blanket bogs) are typical of those occurring in the west Highlands of Scotland, and elsewhere on the Atlantic seaboard of northern Europe although there are some unusual varieties of species-rich heath present on basic soils. The species-rich *Nardus* grasslands are fairly typical in species composition when compared to the community in other parts of Scotland (Pearman *et al.* 2008, JNCC 2013b).

The dominance of wet heath and blanket bog is common to the west Highlands, but contrasts with the uplands in more central and eastern areas of Scotland where dry heath is more dominant. Muirburn is also a greater influence on plant communities in the central and eastern Highlands. Deer home ranges are smaller on Rum than in eastern areas of Scotland and this difference in ranging behaviour might underlie differences among regions in the strength and scale of the influence of the presence of grassland on distribution of grazing (Clutton-Brock *et al*. 1982). The grazing regime on Rum also differs from many other areas in that there are no rabbits, hares or voles on Rum (SNH 2009).

Having noted these possible causes that may underlie contrasting results elsewhere, I found similar results to the one large scale study of the influence of proportion of grassland on browsing of heather that was carried out in central and eastern Highland areas (Palmer *et al*. 2003). This suggests that the influence of grassland on the spatial pattern of deer grazing at larger scales (100-1000s m) is likely to be a general one across open upland communities in the UK, and probably further afield. It might be expected that the scale of influence differs however, due to differences in deer home range size.

6.4 Further research

Changes in spatial pattern of grazing following grazing reduction

Ideally the experiment in which I reduced grazing intensity would have been carried out over a longer period and with greater replication. Extending the study to the heath communities would also have been desirable. Lack of budget and difficulty in identifying suitable sites were obstacles in increasing replication. Given that this study found relatively slow responses in the grassland communities, despite them being quite highly productive, it is unlikely that there would be much change in the less productive heath communities over such a short time period. Any such research should be planned with a decades-long timeframe in mind.

The small scale of the experimental studies meant that I could not directly address changes in the spatial pattern of grazing that would be likely to develop if a reduction in deer numbers occurred over a larger area. An alternative, preferable, approach to examining the effect of reduced grazing on a mosaic of communities would be to cull deer within the boundaries of a larger area, or several unconnected areas, and monitor the effects on multiple communities over a longer time period. This would also allow the change in spatial pattern of grazing in response to changes in deer density to be monitored, if monitoring sites were chosen carefully to include for example, edge and distant regions from community boundaries and tall/short areas of grasslands.

I attempted to address the question of possible changes in spatial pattern in response to deer density differences in Chapter 4, by looking at interactions between deer density and the area of grassland in the locality. However, few interactions were found and these had small explanatory power and, worse, led to predictions which were not interpretable, i.e. predicting less grazing impacts at higher deer densities. Variation in deer density at the scale measured was perhaps not great enough to cause a notable difference in grazing impacts between areas, especially if the relationship with small scale impacts is noisy, and the presence of other herbivores or underlying differences in microclimate or soil fertility across the island might have been influential. An approach that measured deer density or habitat occupancy at multiple scales, perhaps by dung counts, would allow an assessment of what scale(s) deer density is informative about grazing impacts.

As an alternative to the experimental approach, expansion of such an analysis to a larger dataset encompassing a greater number of sites with greater variation in deer density would have greater potential to disentangle the effects of deer density and other factors, as well as having the advantage of greater generality. Habitat impact assessment data from standard monitoring is a viable candidate for such analysis as it is available for many protected sites[3]. Data of this type have previously been used in a large scale study of the effects of different herbivore presence and density on grazing impacts (Hope *et al.* 1996).

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[3] Albeit there will be error due to differences in observers between sites, which would limit comparability (MacDonald, 2010).

Seasonal effects

Large herbivores in seasonal environments commonly alter their range, habitat use and relative preferences for different plant communities seasonally (Welch 1984, Gordon 1989c, Milner *et al.* 2002, van Beest *et al.* 2010b). Range movement may occur in response to harsh weather conditions (Oosenbrug & Theberge 1980, Mysterud *et al.* 2001, Milner *et al.* 2002); apparent shifts in preferences within winter range compared to summer range are often attributable to reduced digestibility of deciduous species (Armstrong *et al.* 1997), and/or the depletion of preferred forage outside the growing season, necessitating a switch to alternative resources (e.g. Grant & Campbell 1978, Welch 1984, Gordon 1989c, Milner *et al.* 2002, van Beest *et al.* 2010b). This results in plant species and communities that are heavily selected for during summer becoming selected less in the winter (Gordon 1989b, Milner *et al.* 2002, van Beest *et al.* 2010b). This is likely to have consequences for the spatial pattern of grazing on other communities; logic suggests that as the previously most preferred resource becomes less used (due to depletion, or to lower quality of a deciduous resource in winter), patterns of grazing on the less productive community in the winter range will be less dependent on the proximity to preferred community, and may instead become centred on areas of abundant, if low quality, forage (van Beest *et al.* 2010b).

Grazing in different seasons can have different outcomes for plant community composition (Hulme *et al.* 2002). Winter grazing can be especially important for heath communities, as this is when heaviest grazing on dwarf shrubs usually occurs (Mitchell *et al.* 1977, Armstrong *et al.* 1997).

A comparative study of the pattern of grazing with respect to vegetation pattern in summer and winter, to determine the differences in influences on spatial pattern of grazing in summer and winter, would give a fuller picture of influences of grazing patterns and overall impact on plant communities.

6.5 Conclusion

Managing mosaics of plant communities of conservation value for individual community conservation targets is inherently difficult.

The results presented in this thesis showed that short-term reduction or exclusion of grazing on preferred communities, which might be implemented to protect the less preferred community, can severely impact the conservation value of the preferred community. Grazing reductions have a wide range of impacts on the preferred community, depending on initial species composition and productivity of the sward, making it difficult to predict the impact of management changes over larger areas.

I also found that the spatial distribution of habitats served to increase conflict in managing for different communities in areas with a high proportion of the preferred community. So management changes will have different impacts in different community contexts.

Conservation management of mosaics therefore needs to aim at pragmatic targets, allowing for compromise of some communities where necessary; the goal should be to optimise the condition of the mosaic, rather than meeting individual conservation targets for each community, as the mosaic composition will affect the outcome of management.

Appendix I Isle of Rum Vegetation maps

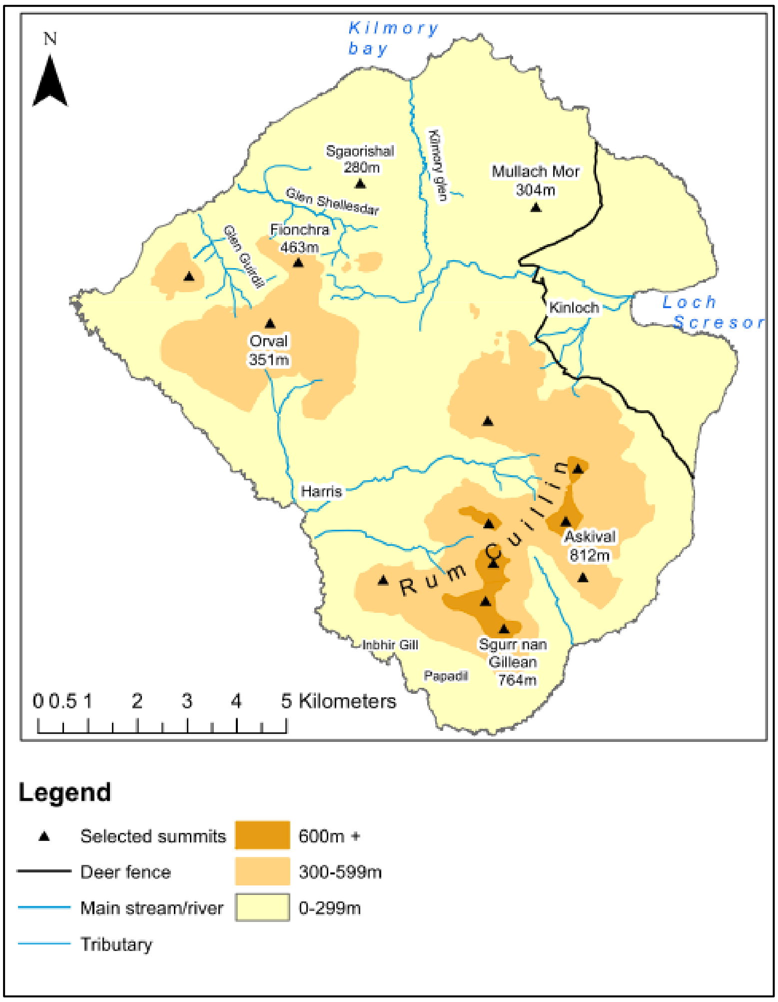

Fig I.1: Place names referred to in description of vegetation change between vegetation mapping in 1964- 1970 and 1998.

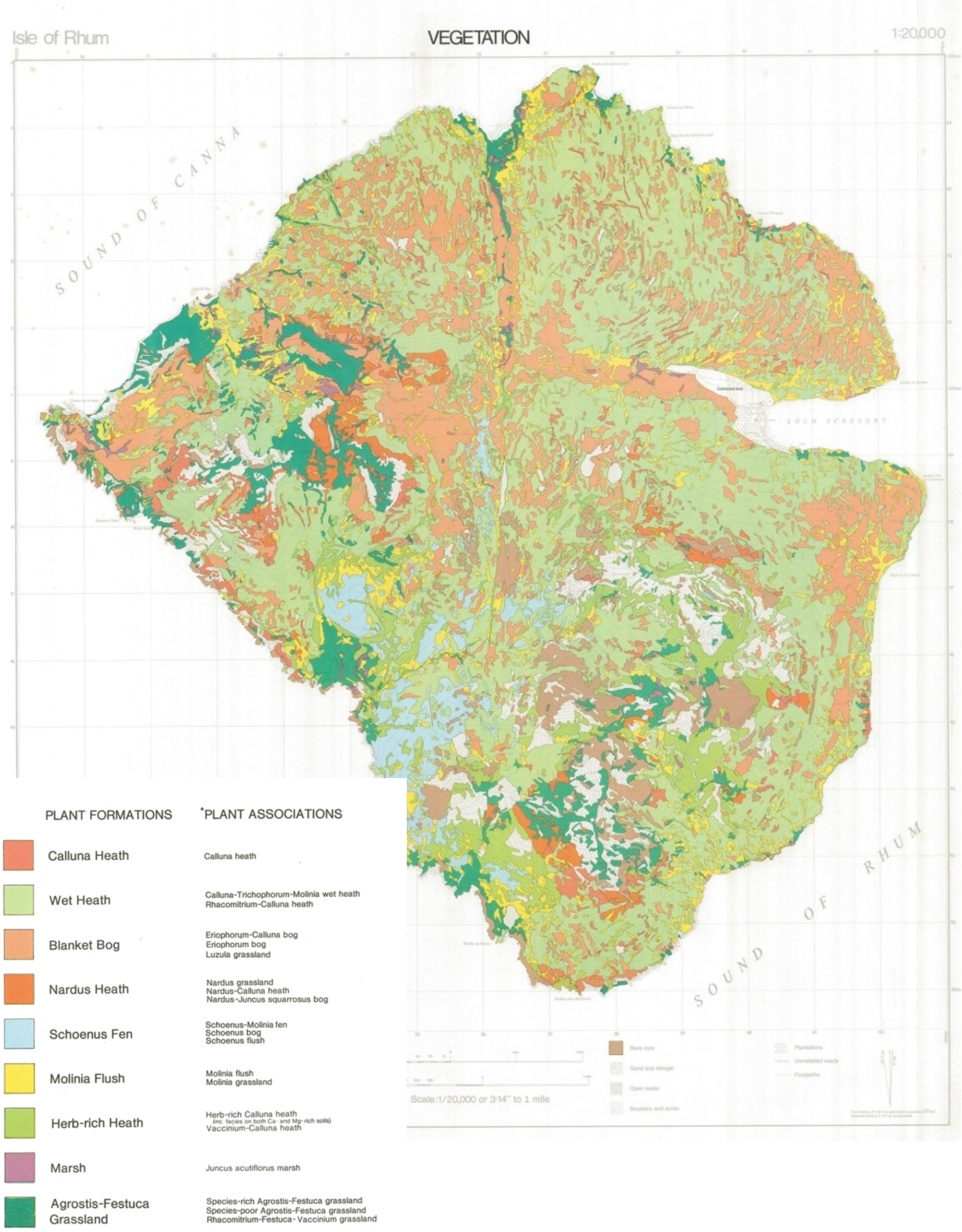

Fig I.2: Map reproduced from Ferreira (1970), with enlarged legend. Plant associations to formations are as follows Calluna heath =*Calluna* Heath; Wet heath =*Calluna Trichophorum Molinia* wet heath, *Racomitirium Calluna* heath; Blanket bog = *Eriophorum Calluna* bog, *Eriophorum* bog, *Luzula* grassland; *Nardus* heath = *Nardus* grassland, *Nardus-Calluna* heath, *Nardus-Juncus squarrosus* bog; *Schoenus* Fen= *Schoenus –Molinia* fen, *Schoenus* bog, *Schoenus* flush; *Molinia* flush = *Molinia* flush, *Molinia* grassland, Herb-rich heath= Herb rich *Calluna* heath, *Vaccinium - Calluna* heath; Marsh = *Juncus acutilfloris* marsh; *Agrostis Festuca* grassland = species rich *Agrostis Festuca* grassland, species-poor *Agrostis Festuca* grassland, *Racomitrium – Vaccinium – Festuca* grassland

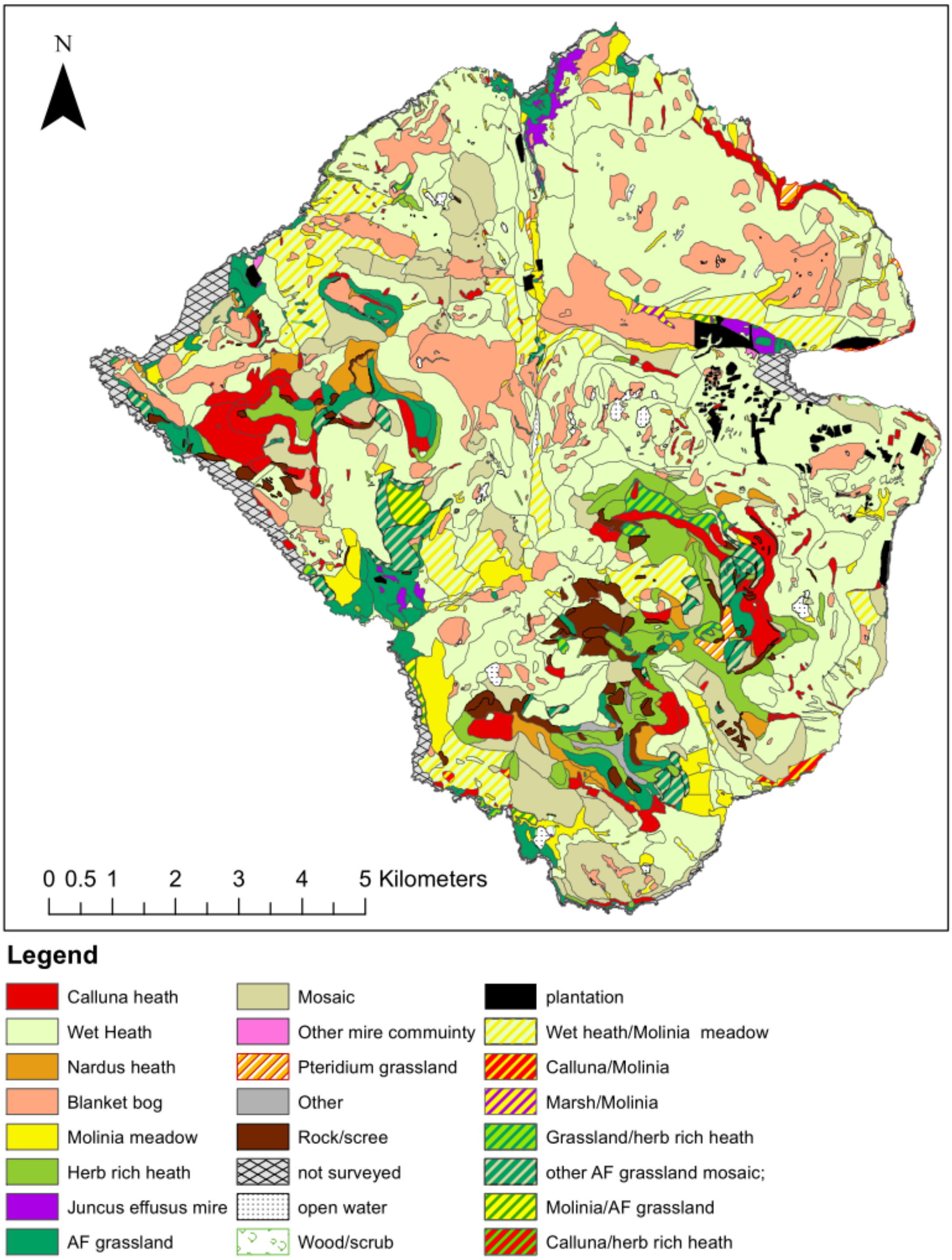

Fig I.3 Map adapted from Bates et al. (2002), with vegetation communities grouped to be as closely comparable with Ferreira (1970) as possible. Select two-community mosaics are shown as a hatched area with colour corresponding to the communities present. Multi-community mosaics containing *Agrostis-Festuca* grassland (AF grassland) are also highlighted. Other mosaic areas are not differentiated and are shown in beige.

Comparison of maps

Some of the differences in appearance between the early and later maps are due to differences in community division and the method of dealing with finely interspersed areas of communities. The main ones are:

1. Many small areas of different community types are differentiated in Feirreia 1970 (Fig I.2). By contrast, in Bates *et al.* (2002) fewer and larger areas are recorded, with multiple community types assigned to areas containing a fine mix of communities (mosaics) (Fig I.3).
2. For clarity, areas recorded as a mix of plant community and rock or scree in Bates et al are coded according to the plant community, this explains the apparent decrease in area of bare rock/scree.

There are few obvious changes in community distribution. The main changes are described below, with the focus on *Agrostis-Festuca* grassland.

***Agrostis-Festuca* grassland:**

Of the low-lying *Agrostis-Festuca* grassland areas, some small areas have been lost over the time period, largely being replaced by *Molinia* dominated grassland or herb-rich heaths. An area of approx. 14 ha of *Agrostis-Festuca* grassland on the coast around Inbhir Gill (see Fig I.1 for location of named places) near Papadil, has been replaced by a mix of herb rich heath and wet, *Molinia* heath. Loss of an area to the North-East of the *Agrostis-Festuca* grassland on Fionchra (~7ha) is apparent. There are also losses of at least 5ha in Glen Guirdil and some smaller areas in Glen Shellesdar (several areas up to 1.5 ha each), mainly replaced by M25, a *Molinia* dominated community. Similarly small areas were replaced by *Molinia* dominated grassland M25, in south Kilmory glen. Conversely, there has apparently been a slight increase in *Agrostis-Festuca* grassland at Harris (perhaps due to the continued intense grazing by cattle, deer, goats and ponies in the area): in the 1998 map *Agrostis-Festuca* grassland is marked as part of a mosaic of community types in an area to the north of the main grassland area whilst it was not recorded in the same area in 1964 (Fig I.2, Fig I.3). In the north of Kilmory Glen there appears to have been a slight expansion of the most westerly section of coastal grassland.

Small areas of coastal grassland on the NW and NE coasts have changed to species rich-heath over the time period, and vice-versa. Of the higher elevation grasslands on Orval and the Rum Cuillin, there appears to have been some interchange between species-rich heath and *Agrostis-Festuca* grassland, however some of the difference may be more apparent than real, due to differences in mapping resolution. In any case there appears to be little loss or gain of either community type. On Orval however, there appears to have been some loss of grassland to be replaced by *Calluna*-dominated and herb-rich heaths.

Changes in other communities

Marsh appears to have replaced *Molinia* flush in Kilmory glen. The community M23 (*Juncus effusus/acutiflorus-Galium palustre* rush-pasture) was assigned to the *Juncus acultifloris* marsh category; however, *Molinia* can also be present in the sward. M25 (*Molinia caerulea-Potentilla erecta* mire) was assigned to the 'Molinia flush' category; this community is dominated by *Molinia*, but can contain *Juncus acutifloris*. The flora of some M23 and M25 sub-types can be otherwise quite similar (Rodwell, 1992), so the transition of much of the '*Molinia* flush' in Kilmory Glen to 'Marsh' represents a change in the dominance of these two species between the time periods. The other main changes are plantations in various locations around the island, especially inside the deer fenced area in the East of the island (see Fig I.1 for deer fenced area). Here the coastal grasslands have been replaced by *Pteridium* dominated communities or heath (Fig I.2, Fig I.3).

In the Bates *et al* (2002) data, there are no distinct NVC community(s) recorded that obviously correspond to the description of *Schoenus* fen. Ball (1998 Unpublished) attributed this community to the M14 (*Schoenus nigricans –Narthecium ossifragum* mire) NVC community, which is not recorded anywhere on Rum in the 1998 survey. This community appears to no longer exist, then, replaced mainly by M15 (*Trichophorum cespitosum-Erica tetralix* wet heath) and M25 (*Molinia caerulea-Potentilla erecta* mire). This suggests that the main change in composition has been an increase in *Molinia* dominance on these communities, resulting in a shift in community classification – M14 can contain abundant *Molinia*, but *Schoenus* is dominant. It is possible that the *Schoenus* fen community would also correspond to a variant of the M15a sub-community (Rodwell 1992) which can contain much *Schoenus* and has some of the same associated species, so some small areas of similar community may still exist. The decline in *Schoenus* fen/M14 as a distinct type can perhaps be attributed changes in grazing pressure, in particular the reduction in grazing following the removal of sheep from the island. Between 1957 and 1972, *Schoenus* fen showed an increase in Molinia dominance and a corresponding decline in *Schoenus* and most other species. By 1972, % cover of *Molinia* already exceeded that of *Schoenus* in the grazed plot (Ball 1974).

Following the introduction of cattle grazing Ball & Hirst (1994) reports a decline in *Shoenus* on '*Molinia* flush' and 'Marshes' (this is different terminology to that used in Ball (1998 Unpublished), thus it is not clear exactly which of the Ferriera classes or NVC communities these refer to); an increase in *Molinia* and decline in *Schoenus* on wet communities was noted in an earlier report (dated 1980) referred to by Ball & Hirst (1994). Ball & Hirst (1994) tend to attribute changes in this period (1972-1993) to the introduction of cattle, however in the case of the continued increase of *Molinia* on the wetter communities up until the 1980s (little further increase in *Molinia* was recorded in the 1993 resurvey (Ball & Hirst 1994)) the continued effects of recovery from heavy sheep grazing seem a more likely cause. The cessation of burning may also have influenced the spread of *Molinia* (Ball 1974). Since *Schoenus* fen mainly occurred in Harris Glen there is very little 'control' area where *Schoenus* dominated communities occurred and cattle were not present; however, there were some smaller patches near Papadil which is not accessible to cattle and these have also disappeared (replaced largely by M15a), also suggesting that cattle grazing is not responsible.

Appendix II Species lists and list of abbreviations of species names

List of abbreviations of species names used in the thesis. Latin Names follow Stace (2010) for vascular plants and (Smith & Smith 2004) for bryophytes.

Vascular plants
Agrocapi= Agrostis capillaris
Agrostol= A. stolonifera
Antedioi =Antennaria dioica
Anthodor = Anthoxanthum odoratum
Callvulg= Calluna vulgaris
Carearen = Carex arenaria
Careflac= C. flacca
Dactmacu = Dactylorhiza maculata
Festrubr =Festuca rubra
Festovin = Festuca ovina/vivipara
Heirpilo = Pilosella officinarum
Koelmacr = Koeleria macrantha
Lotucorn = Lotus corniculatus
Luzucamp = Luzula campestris
Nardstri = Nardus stricta
Plancoro = Plantago coronopus
Planlanc=P. lanceolata
Planmari= P. maritima
Poa_prat =Poa pratensis
Prunvulg = Prunella vulgaris
Poteerec= Potentilla erecta
Thympoly =Thymus polytrichus
Trifrepe= Trifolium repens
Ranuacri= Ranunculus acris

Bryophytes
Hylosple = Hylocomium splendens
Homalute = Homalothecium lutescens
Mniumarg = Mnium marginatum
Rhytsqua = Rhytidiadelphus squarrosus
Thuitama = Thuidium tamariscinum

Full species lists

List for sites in Chapter 2

Vascular species

Alchemilla millifolia
Agrostis capillaris
Agrostis stolonifera
Antennaria dioica
Anthoxanthum odoratum
Arrhenatherum elatius
Arctostaphalus uva-ursi
Bellis perennis
Botrychum lunaria
Calluna vulgaris
Campanula rotundifolia
Carex arenaria
Carex flacca
Carex nigra
Carex pilicaris
Centurea nigra
Cerastium fontanum
Cynosorus cristatus
Dachtylorhiza maculata
Danthonia decumbens
Daucus carota
Eric cineria
Erica tetralix
Empetrum nigra
Equisetum palustris
Euphrasia officianalis
Festuca rubra
Festuca ovina
Galium saxatile
Galium verum
Pilosella officanarum
Holcu lanatus
Hypercium pulchrum
Koeleria macrantha
Leontodon autumnalis
Linum catharticum
Lotus corniculatus
Luzula campestris
Luzula multiflora
Molinia caurelea
Nardus stricta
Parnassia palustris
Pedicularis palustris
Plantago coronopus
Plantago lanceolata
Plantago maritima
Poa pratensis
Polygala serpyfolia
Polygala vulgaris
Potentilla erecta
Prunella vulgaris
Ranunculus acris
Ranunculus repens
Rhinanthus minor
Sagina procumbens
Selegenella selaginoidies
Succisa pratenses
Taraxacum officianalis
Thymus polytrichus
Trifolium pratenses
Trifolium repens
Veronica serpyfolia
Veronica officianalis
Viola canina
Viola riviana

List from experimental sites detailed in Chapter 3

Vascular species

Alchemilla millifolia
Agrostis capillaris
A. stolonifera
A. canina
Aira praecox
Ammophila arenaria
Anthoxanthum odoratum
Arrhenatherum eliatus
Anthyllis vulneria
Arrhenatherum eliatus
Bellis perennis
Botrychum lunaria
Calluna vulgaris
Campanula rotundifolia
Carex arenaria
C. flacca
C. nigra
C. panicea
C. pilulifera
C. pulicaris
Centurea nigra
Cerastium fontanum
Cynosurus cristatus
Dactylis glomerata
Dachfuch
Danthonia decucumbens
Daucus carota
Equisetum arvensis
E. pratensis
E. palustris
E. variegatum
Erica cinerea
Euphrasia officianalis agg.
Festuca ovina/vivipara
F. rubra
Galium saxatile
G. palustris
G. verum
Gentianella campestris
Helichtrichon = (Avenula) pubescens
Heiracium.spps
Holcus.lanatus
Hypercium pulchrum
Juncus articulatus
Koleria macrantha
Lathyrus linifolius
Leontodon autumnalis
Linum carthicum
Lolium perenne
Lotus corniculatus
Luzula campestris
Medicago lupilina
Molinia caurelea
Nardus stricta
Orchid spps
Parnassia palustris
Pedicularis spps
Pinguicula vulgaris
Plantago coronopus
P. lanceolata
P. maritima
Poa pratensis
Polygala serpyllifolia
P. vulgaris
Potentilla erecta
Primula vulgaris
Prunella vulgaris
Pteridium aquilinum
Ranuculus acris
R. ficaria
R. repens
Rhinanthus minor
Rumex acetosa
Sagina procumbens
Selaginella selaginoides
Succisa pratensis
Taraxacum.off.
Thymus preacox
Trifolium dubium
T. pratenses
T. repens
Veronica officianalis
Viola palustris
V. riviana
Vicia cracca

Bryophytes

Atricum undulatum
Breutelia chrysoscoma
Callergionella cuspidatum
Campylium stellatum
Campylopus atrovitens
Cladonia spps.
Climacium.dendroides
Ctenidium molluscum
Dicranum majus
D. scoparium
Ditrichum gracile
Fissidens spps.
Homolothecium lutescens
Homalothecium sericium
Hylocomium splendens
Hypnum compressiforme
Hypnum lacunosum
Kindbergia prealonga
Mnium hornum
M. marginatum
Peltigaria.spps
Polytrichum juniperium
Pseudoscleropodium purum
Rhodobryum roseum
Rhytdiadelphus loreus
R. squarrosus
R. triquetrus
Syntricia ruralis (sub-sp.*ruralis*)
Sphagnum spps.
Thiudium delictilum
Thuidium tamariscinum

Appendix III Grazing exclusion, results of one season's exclusion.

The effect of exclusion for one season was tested. This analysis uses all plots present at the each site; that is, one control and two exclusion plots (see Fig 2.2). Treatment x time interaction was tested as in Chapter 2, using linear mixed effects models with the fixed effect Treatment x Time and random effect of Site. Poisson errors were used for species number models.

There was no significant effect of exclusion on litter, bare ground, diversity or species number.

Table III.1: Effect of grazing exclusion for one season on diversity and structural measures.

Response	Fixed effects	Coefficients	S.E.	P value of interaction
Shannon index	Intercept	1.86	0.059	
	Cage	0.003	0.079	
	Time	-0.416	0.066	
	Cage*Time	0.098	0.112	0.370
Log(Litter)	Intercept	2.24	0.119	
	Cage	-0.042	0.118	
	Time	0.713	0.098	
	Cage* Time	-0.150	0.167	0.374
Log(Bare ground+.1)	Intercept	-0.19865	0.280	
	Cage	0.0783412	0.376	
	Time	-1.3019	0.311	
	Cage* Time	-0.248	0.531	0.641
Gram spps	Intercept	1.33	0.107	
	Cage	-0.077	0.179	
	Time	-0.071	0.154	
	Cage* Time	0.107	0.262	0.684
Herb spps	Intercept	2.30	0.070	
	Cage	-0.113	0.109	
	Time	0.009	0.093	
	Cage*Time	0.253	0.160	0.114

Appendix IV Reduced grazing experiment additional data

Table IV.1: Effect of reduced grazing as measured by dung count on diversity and structural measures. The model is y~ Month+ Time + dung count. Site was included as a random effect. Dung count is the total cumulative count of pellet groups, except for utilisation of *Festuca* and *Calluna,* which are based on seasonal cumulative counts with a season deemed to start in March, so that the utilisation is compared to the dung accumulated between the previous March and the time of measurement. Time is number of months since start.

Response	**Fixed effects**	**Coefficient**	**S.E.**	**p-value**
Bare ground	Intercept	-1.31	0.444	0.783
	Dung	$2.06e^{-3}$	$6.25\ e^{-3}$	
	Time	0.010	0.014	
	March (vs. July)	0.528	0.200	
	Nov (vs. July)	0.200	0.222	
Log(Litter)	Intercept	1.11	0.176	0.628
	Dung	$-2.22\ e^{-3}$	$4.472\ e^{-3}$	
	Time	0.043	0.010	
	March (vs. July)	1.70	0.148	
	Nov (vs. July)	1.18	0.164	
Shannon (Vascular plant species only)	Intercept	2.04	0.065	0.785
	Dung	$4.99\ e^{-4}$	$1.76\ e^{-3}$	
	Time	0.0030	0.004	
	March (vs. July)	-0.301	0.059	
	Nov (vs. July)	-0.442	0.066	
Herb cover	Intercept	3.27	0.240	
	Dung	$6.60\ e^{-3}$	$3.69\ e^{-3}$	0.069^{+}
	Time	-0.019	0.009	
	March (vs. July)	-1.25	0.118	
	Nov (vs. July)	-1.16	0.131	
Cover of graminoids	Intercept	4.09	0.125	0.811
	Dung	$-4.50\ e^{-4}$	$1.92\ e^{-3}$	
	Time	-0.015	0.004	
	March (vs. July)	-0.583	0.061	
	Nov (vs. July)	-0.207	0.068	
Herb species no	Intercept	20.9	1.30	0.451
	Dung	$1.30\ e^{-2}$	$0.018\ e^{-2}$	
	Time	$1.04\ e^{-4}$	0.041	
	March (vs. July)	-4.32	0.567	
	Nov (vs. July)	-4.26	0.630	

Table VI.1: cont.

Response	Fixed effects	Coefficient	S.E.	p-value
Graminoid spps no	Intercept	14.5	0.671	
	Dung	**-2.75 e^{-2}**	1.22 e^{-2}	**0.023***
	Time	0.104	0.028	
	March (vs. July)	-4.01	0.392	
	Nov (vs. July)	-4.20	0.435	
Festuca utilisation	Intercept	0.110	0.027	0.380
	Dung	-5.90 e^{-4}	6.87 e^{-4}	
	Time	0.002	0.001	
	March (vs. July)	0.023	0.022	
	Nov (vs. July)	0.058	0.025	
Poa utilisation	Intercept	0.208	0.033	0.111
	Dung	-1.12 e^{-3}	7.11 e^{-4}	
	Time	6.35 e^{-4}	8.58 e^{-4}	
	March (vs. July)	0.002	0.024	
	Nov (vs. July)	0.218	0.026	
Calluna utilisation	Intercept	7.63	2.84	
	Dung	**-0.138**	0.069	**0.051^{+}**
	Time	0.214	0.091	
	March (vs. July)	33.6	2.80	
	Nov (vs. July)	23.0	3.10	

Appendix V Deer and Goat numbers on Rum

V: i Full list of deer densities and deer per km^2 *Agrostis- Festuca* grassland from 1996 - 2008

Table V.1: Deer densities by block from 1996-2008. *2003 uses interpolated values

Year	DMB1	DMB2	DMB3	DMB4	DMB5
1996	17.5	12.7	16.4	26.7	2.9
1997	17.5	12.7	16.4	26.7	2.9
1998	19.7	13.6	14.1	22.2	2.9
1999	18.2	11.5	16.7	23.6	4
2000	17	10	18.7	20.4	2.2
2001	17.5	6.6	13.6	17.8	2.2
2002	15.7	7.3	13.6	12.5	1.2
2003*	20.4	8.6	15	11.2	1.9
2004	25.1	9.9	16.3	9.8	2.5
2005	21.6	10.8	15.3	12.2	2.6
2006	17.8	8.2	14.8	15.8	1.8
2007	15.7	7.7	14.3	9.8	0.7
2008	15	7.3	12.3	11.1	2.4

Table V.2: Deer km^{-2} grassland by block from 1996-2008. *2003 uses interpolated values

Year	DMB1	DMB2	DMB3	DMB4	DMB5
1996	317	145	247	1090	81
1997	357	155	213	902	81
1998	386	153	222	1100	67.1
1999	330	131	252	958	113
2000	308	114	281	828	62.5
2001	317	74.8	204	721	62.5
2002	285	83.7	205	508	34.7
2003*	371	98.4	226	454	53.2
2004	456	113	246	399	71.7
2005	392	123	231	494	74
2006	323	93.5	223	640	50.9
2007	284	87.9	216	399	20.8
2008	272	83.7	186	452	67.1

V: ii Isle of Rum Goat census 2010

Fig V.1: Routes taken for goat census, 2010. Ordnance survey data used under © Crown Copyright and Database Right 2014. Ordnance Survey (Digimap Licence)

Table V.3: Goat census 2010, numbers by census route and sex/age category

	Adult ♂	Adult ♀	Yearling ♂	Yearling ♀	Kid	TOTAL
Harris	36	35	4	4	19	**98**
Papadil 1	6	37	0	0	17	**60**
Shellesder	14	3	0	0	1	**18**
Sgorr Reidh	27	53	6	0	21	**107**
Papadil 2	10	39	6	2	19	**76**
						359

Appendix VI Additional information for Chapter 4

VI: i Distribution of plots by deer block and mean and range of elevation of plots

Table VI.1: Distribution of plots by deer block, and mean and range of elevation of plots

Community	No. of plots at set-up	No. of plots in each deer block		Mean elevation	SE	Median elevation	Range of elevation
Grassland	94	**DMB1**	13	172m	15.8	124m	8m-537m
		DMB2	51				
		DMB3	12				
		DMB4	16				
		DMB5	2				
Wet Heath	65	**DMB1**	12	222m	11.4	210m	42m-491m
		DMB2	19				
		DMB3	11				
		DMB4	0				
		DMB5	21				
		DMBX	2				
Dry Heath	91	**DMB1**	15	232m	12.4	211m	39m-464m
		DMB2	20				
		DMB3	26				
		DMB4	19				
		DMB5	10				
Alpine Heath	50	**DMB1**	7	469m	21.1	500m	42m-754m
		DMB2	19				
		DMB3	13				
		DMB4	4				
		DMB5	7				
Alpine Heath **without DMB4**	46	**DMB1**	7	505m	13.2	503m	294m-754m
		DMB2	19				
		DMB3	13				
		DMB5	7				

VI: ii Spatial Autocorrelation: methods

Spatial autocorrelation (SAC) was tested for using the 'Variogram' function in the package nlme. The significance of SAC was tested using Moran's I in spdep package (Bivand 2013). Where the Moran's I test indicated that the model still had significant SAC after adding interaction terms and/or blocking by DMB, the Variogram function was used to check whether SAC had improved, in which case the change was accepted.

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