RESTORATION AND MANAGEMENT OF WILDFLOWER-RICH MACHAIR FOR THE CONSERVATION OF BUMBLEBEES

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Abstract

Over the last half century, the widespread decline of bumblebees across the agricultural landscapes of Western Europe and North America has been well documented. This decline has undoubtedly been driven to a large extent by the intensification of agriculture, which has fragmented landscapes and removed large areas of suitable foraging habitat, nesting and hibernation sites. Consequently, some of the rarest *Bombus* species now persist only in isolated pockets of semi-natural habitat, which have been subjected to little agricultural intensification. Of the 25 *Bombus* species native to the UK, three species have gone extinct in recent decades and several others are severely threatened. Remaining populations of the UK's rarest bumblebee, *Bombus distinguendus*, have become strongly associated with florally-rich machair grassland habitats found only in the North and West of Scotland and Western Ireland. Machair, a unique habitat that forms on soils rich in shell sand, has been maintained by rotational agricultural practices implemented by crofters. However, recent changes in crofting practices, which include the intensive grazing of machair in some areas, or conversely the abandonment of machair management all together in others, have resulted in sections of machair that have become degraded and consequently exhibit low floral abundance and species diversity. This has significant implications for species such as *B. distinguendus*, which have for the most part come to rely of the florally-rich swards of machair grassland. This thesis aimed to develop a greater understanding of how machair grassland habitats are utilised by foraging bumblebees, including *B. distinguendus*, and in turn examined the potential for restoring degraded areas of machair via a variety of methods. The research presented here examines the influence of current crofting practices on the abundance of bumblebees and their forage plant species and combines this information with a detailed exploration of the machair seed bank and potential machair restoration treatments. The specific foraging requirements of *B. distinguendus* were found to be similar to those of other long-tongued bumblebee species and the provision of plants from the Fabaceae family was found to be of particular importance. Current crofting practices implemented in the North and West of Scotland were, on the whole, found support low numbers of foraging bumblebees. Similarly, existing habitat management schemes, designed to provide early cover for corncrakes and foraging resources for bumblebees, were found to be largely ineffective in attracting *B. distinguendus*, when compared with florally-rich machair habitat. In addition, this research suggests that the existing machair seed bank is unlikely to provide a sufficient resource for reinstating florally-rich habitat to degraded areas of machair. However, this thesis has demonstrated that it is possible to implement seed mixes on machair which can reinstate species typical of machair plant communities and which also attract high numbers of foraging bumblebees. The findings of these habitat assessments and restoration trials are examined in full in the following chapters and implications for the future management of wildflower-rich machair are discussed throughout.

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Declaration

I declare that this thesis has been composed by myself and embodies the results of my own research. Where work was carried out in collaboration with others, I have acknowledged the nature and extent of their work.

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Nicola Redpath

1 General introduction

1.1 The decline of bumblebees

Bumblebees are arguably among the most charismatic of invertebrate organisms and they are undoubtedly some of the most important and well adapted pollinators of both wildflowers and commercial crops (Osborne & Williams 2001; Bäckman & Tiainen 2002; Carreck & Williams 2002; Carvell 2002; Bhattacharya *et al*. 2003; Dramstad *et al*. 2003; Goulson 2003; Darvill *et al*. 2004). In combination, their endearing aesthetics and economically beneficial pollinating services render these creatures inherently appealing to a wide audience.

Despite their popularity, many bumblebee species have undergone significant declines in recent decades and of the twenty five species native to the UK, three are now believed to have gone extinct and several other species have become seriously threatened (Williams 1982; Goulson 2003; Benton 2006). Seven of the most endangered *Bombus* species, approximately one third of the UK's remaining bumblebee species, are now listed as UK Biodiversity Action Plan priority species. Competition from introduced species and pathogen spillover from commercially reared colonies have been identified as possible factors contributing to the decline of bumblebees, particularly in North America (Edwards 1997; Colla *et al.* 2006; Williams *et al*. 2007; Goulson *et al.* 2008a; Goulson 2010). However, most authors agree that the primary driver of declines in Europe has been the widespread and well documented intensification of European agriculture, which has taken place over the last half century (Carvell *et al*. 2007; Goulson *et al*. 2008a).

1.2 Agricultural intensification

Agriculture can be defined as the science or practice of cultivating the soil and rearing animals (Oxford English Dictionary, 1995) and at present more than 70% of the UK's landmass is involved in some form of agricultural enterprise (Carreck & Williams 2002; DEFRA 2007).

The rapid intensification of agricultural practices, a phenomenon experienced by much of Western Europe since the late 1940s, has been associated with a widespread decline in farmland biodiversity and in particular the decline of many farmland bird species (Chamberlain *et al*. 2000; Vickery *et al*. 2001). The onset of agricultural intensification was catalysed by the end of the Second World War as Britain was encouraged to strive for self sufficient food production through the introduction of the Agriculture Act of 1947. Subsidies were granted to farmers who improved outputs by adopting new farming practices and increased agricultural efficiency (Robinson & Sutherland 2002; Goulson *et al*. 2008a).

Over the last sixty years, agricultural practices have become increasingly refined in order to satisfy the demand for greater efficiency and productivity and consequently traditional farming methods have, to a large extent, been abandoned (Robinson & Sutherland 2002). New farming strategies have been facilitated by numerous technological advances including the production of sophisticated farm machinery, the availability of cheap, inorganic fertilizers and the development of pre-emergent herbicides (Green 1990; Chamberlain *et al*. 2000). In combination, these agricultural advances have considerably reduced the necessity for human labour. This has in turn been reflected by a substantial decrease in the UK's agriculturally related work force, which has reduced by almost 80% since the 1940s, even though the majority of the UK landmass remains under some form agricultural influence (Robinson & Sutherland 2002).

With such a large proportion of land involved in agricultural production it is inevitable that changes in agricultural practice will have repercussions for the species which exist within the farmed landscape. Thus agricultural intensification has paralleled, and indeed been held largely responsible for, a notable decline in farmland biodiversity (Chamberlain *et al*. 2000; Bäckman & Tiainen 2002). Bumblebees in particular, have suffered their greatest decline in the intensively cultivated regions of Europe (Osborne & Williams 2001; Carreck & Williams 2002; Carvell *et al*. 2007).

1.2.1 Habitat loss and fragmentation

The need to increase field sizes in order to accommodate larger, more complex farm machinery has led to the removal of non-crop habitats including hedgerows, semi-natural, unimproved grasslands and field margins, thus reducing the heterogeneity of the wider farmed landscape (Chamberlain *et al*. 2000; Söderström *et al*. 2001; Bäckman & Tiainen 2002; Robinson & Sutherland 2002; Weibull *et al*. 2003). The removal of these habitats for the purpose of improving agricultural efficiency is believed to have had a negative impact on bumblebee populations by reducing the quantity of available forage material and also by removing potential nesting and hibernating sites (Osborne & Williams 2001; Bäckman & Tiainen 2002; Carreck & Williams 2002; Bhattacharya *et al*. 2003; Edwards & Williams 2004; Carvell *et al.* 2007).

Not only does this loss and fragmentation of habitat directly remove resources, but it also reduces the availability of ‘corridors’ that link suitable resource patches within the agricultural matrix. This in turn restricts the movement of a range of species through the farmed landscape (Söderström *et al*. 2001). Whilst bumblebees do not necessarily require corridors in order to traverse the landscape, when habitats become fragmented by agriculture, road construction, railway development etc., there is evidence to suggest that bumblebees perceive, and avoid these barriers within their environment (Bhattacharya *et al*. 2003). Therefore, as habitat patches become increasingly isolated due to habitat fragmentation, the frequency of bumblebee movements between patches is likely to be reduced (Bhattacharya *et al*. 2003).

Osborne and Williams (2001) examined the site constancy of bumblebees on patches of grass/herb mixture, which varied in size, within a field of barley. Although the mark, release, recapture technique used only recaptured approximately 30% of the bees released, the authors found that bees were more likely to forage constantly on a single resource patch if it was large and surrounded entirely by barley. Movement between resource patches was a more common occurrence if patches of equal size were contiguous with one another, essentially forming one large foraging patch. Although bumblebees are robust flyers and can travel great distances, even the narrowest strips of barley were perceived as a barrier to movement. The forage site constancy demonstrated by bumblebees in this study emphasises the potential of habitat fragmentation to limit the movement of pollinators and consequently restrict pollen dispersal.

Many of the rarest *Bombus* species are now confined to small pockets of semi-natural habitat distributed throughout the agricultural matrix. As existing bumblebee populations become increasingly isolated on remnants of suitable habitat, the risk of genetic isolation increases and populations become more likely to suffer from the negative effects of reduced genetic diversity, including inbreeding and elevated levels of parasitism (Darvill *et al*. 2006; Whitehorn *et al*. 2009; Whitehorn *et al*. *in press*). This not only has implications for bumblebee species, but also the plant species reliant on entomophilous pollination. Cresswell and Osborne (2004) describe how the size, density and spatial isolation of experimental patches of oilseed rape influenced pollinator behaviour, the dispersal of pollen and the reproductive success of plants, with the smaller, more isolated patches being more susceptible to inbreeding.

More detailed research into bumblebee behaviour and pollen flow within the agricultural environment is required. However, there is the distinct possibility that lower seed set due to reduced pollinator efficiency could ultimately change localised plant community composition. This could in turn affect other invertebrate and herbivorous species which rely upon plants for the provision of habitat and/or nutritional resources (Bhattacharya *et al*. 2003; Dramstad *et al*. 2003; Cresswell & Osborne 2004; Darvill *et al*. 2004). Therefore, the loss and disturbance of habitats is recognised as a serious threat to a large number of rare and declining floral and faunal species and protecting, conserving and restoring these habitats has become increasingly important.

1.2.2 The negative impact of herbicides and fertilisers

Another agricultural issue linked with the decline of bumblebees is the use of herbicides. Not only are herbicides extensively and routinely applied to crops and field margins but they are also unintentionally deposited on non-target vegetation via the wind. The use of herbicides to reduce the weed burden of field margins can change their floral composition considerably, removing potential bumblebee forage material from the farmed landscape. Research in Finland has shown that herbicide usage is likely to have contributed to the loss of nearly two thirds of weed flora biomass between the 1960s and 1980s. The loss of weed species not only means the removal of probable bumblebee foraging resources but also potential nest sites (Bäckman & Tiainen 2002).

The use of artificial fertilisers in the management of grassland and crops has had a negative impact on farmland biodiversity by enhancing the growth and prevalence of dominant plant species. In the case of grasslands, an increase in nitrogen supply often promotes the growth of fast growing grass species, which outcompete the slower growing species adapted to nutrient poor soils (Bakker & Berendse 1999). Consequently, the widespread use of inorganic fertilisers is likely to have had a negative impact on bumblebee populations by encouraging the plant species which thrive in highly fertile soils to out-compete bumblebee forage plants. The reduced species diversity of grassland swards, or indeed any habitat which suffers reduced plant species diversity, will inevitably support a lower diversity of species, including bumblebees.

The application of inorganic fertilizers now routinely replaces the use of leguminous crops, which were traditionally grown on a rotational basis because of their nitrogen fixing properties. Whilst this cheaper alternative to rotational cropping may be, at present, a more efficient farming strategy, leguminous species are recognised as important foraging resources for the long-tongued *Bombus* species and the widespread removal of these plants from the farmed landscape has therefore undoubtedly played a significant contributory role in the decline of bumblebees (Goulson *et al*. 2008a).

Ironically, these and other commonplace agricultural practices, are threatening the existence of the very organisms which benefit farmers by increasing the yields of commercial crops as a result of their pollination services (Sih & Baltus 1987; Osborne & Williams 2001). Bumblebees are considered far less sensitive to changes in weather conditions than other pollinating species such as the honey bee (*Apis mellifera*). In a study conducted using experimental patches of *Phacelia tanacetifolia*, the foraging activity of honey bees declined with less favourable weather conditions but there was little change in bumblebee activity, thus highlighting their efficiency as pollinators in variable climates (Dramstad *et al*. 2003).

1.2.3 Grassland management

The removal of non-crop habitats and the use of herbicides have undoubtedly changed agricultural landscapes in such a way that they have contributed to the decline of bumblebees, but it is changes in grassland management that are most likely to have had a negative impact on the rarer species (Goulson *et al*. 2008a).

Perhaps the most significant change in grassland management has been the replacement of wildflower-rich hay meadows with heavily fertilised silage fields (Green 1990; Chamberlain *et al*. 2000; Goulson *et al*. 2008a). The production of silage instead of hay enables farmers to cut grass crops much earlier in the year and several cuts can be taken from a single field. By the 1980s this strategy had become the dominant method of producing grass based livestock forage in the UK (Chamberlain *et al*. 2000).

In enabling the early cutting of grass crops, this form of grassland management often results in the early removal of wildflowers which may be present in the sward. Traditional hay production necessitates that the grass crop is cut later in the year and wildflower species present in the sward are able to persist throughout the season, providing patches of foraging resources for bumblebees throughout the summer period (Goulson *et al*. 2006). Unlike honeybees, bumblebees only store pollen and nectar for a few days at a time and therefore require continuous access to appropriate forage material throughout the duration of their colony's life cycle (Dramstad *et al*. 2003). The late cutting of grassland habitats also allows wildflowers to set seed before they are removed from the landscape, leaving a legacy of wildflowers and potential bumblebee forage material in the form of seed. The removal of flowering plants early in the year has almost certainly had a negative impact on the survival of bumblebee populations (Walther-Hellwig & Frankl 2000; Goulson *et al*. 2008).

The impacts of agricultural intensification have affected a broad range of taxa and much research has been conducted to assess the disruption to a whole suite of plant and animal species. Chamberlain *et al*. (2000) looked at how agricultural intensification in

England and Wales has affected the abundance of farmland birds. Amongst other findings they noted that the process of under sowing crops with grass or clover, once a widespread practice, had declined significantly with the increasing separation of arable and pastoral enterprises. In the 1940s much of the temporary grassland in the UK would have been one year old clover leys but by the 1980s, some 40 years later, less than 1% of the total area of temporary grassland consisted of clover leys (Chamberlain *et al*. 2000). Despite the beneficial nitrogen fixing properties of clover, these leys are now surplus to requirements due to the ready availability of artificial nitrogenous fertilisers.

A study conducted in Finland in 1996, which attempted to establish the habitat quality of field margins for bumblebees, concluded that one of the most important habitat features for bumblebees was the presence of key forage species at certain times of the year, with clover species identified as key forage plants (Bäckman & Tiainen 2002). As a significant component of the suite of plants utilised by foraging bumblebees, including the UK's rarest species *Bombus distinguendus* (Edwards & Williams 2004), the decline of clover leys in British agricultural systems is likely to be an important contributing factor in the decline of bumblebees.

Goulson *et al*. (2006) argue that the six bumblebee species which remain relatively common throughout the UK continue to be so widely distributed because of their ability to adapt and forage on non-native garden plant species. Conversely, rare and declining bumblebee species may simply be less flexible and are therefore more reliant on native wildflowers. However, over the course of the last 60 years, more than 90 percent of unimproved grassland has been removed from the wider UK countryside (Fuller 1987) and so it is unsurprising that species which rely upon wildflower rich habitats have continued to diminish in number.

Some degree of grassland management can, however, have a positive impact on plant species diversity. Carvell (2002) conducted a study of habitat use by bumblebees on Salisbury Plain Training Area, one of the largest remaining unimproved chalk grasslands in North-West Europe. The author assessed six different grassland management regimes including reverting arable land, unmanaged grassland edges, grassland edges that were regularly disturbed by the passage of military vehicles (disturbed edges), sheep-grazed grassland, recently cattle-grazed and previously cattle-grazed grassland. The lowest mean numbers of bumblebees were recorded on unmanaged edge habitats, which had low floral density. The management type which resulted in the highest abundance of all but one of the *Bombus* species observed was the recently cattle-grazed grassland. Small scale disturbances were also suggested to be important for maintaining floral diversity in an otherwise relatively unmanaged grassland habitat. This study highlights the importance of maintaining appropriate active grassland management in order to ensure the prevalence of bumblebee forage plant species.

By identifying the habitat characteristics that influence the abundance, diversity and foraging activity of various bumblebee species, existing grassland management practices can be manipulated in order to create conservation strategies for specific species and habitats. Restoring grassland habitats for the benefit of bumblebees requires further research. However, grassland restoration is a notoriously complex issue and the diversification of grassland after a period of intensive management has previously proved difficult to achieve (Pywell *et al*. 2007).

1.2.4 Bumblebee conservation within agricultural landscapes

Farmed landscapes are typically areas high in plant density but low plant species diversity. Unsurprisingly, this uniformity is not conducive to high levels of biodiversity and in particular, the diversity of bumblebee species on farmland is positively correlated with plant species diversity (Carreck & Williams 2002). However, a site with high plant species diversity does not necessarily equate to a high abundance of bumblebees as they are known for their foraging consistency to certain flowering species, even if other pollen and nectar producing species are readily accessible to them (Osborne & Williams 2001). In order to meet the foraging requirements of a range of bumblebee species, a habitat must contain a suite of key forage plants.

There is much ongoing debate as to the benefit of mass flowering crops for bumblebees (Westphal *et al*. 2003; Westphal *et al*. 2006; Knight *et al*. 2009; Westphal *et al*. 2009). In the UK, the increasing areas of oil seed rape production for example (Chamberlain *et al*. 2000) provide huge expanses of distinctive yellow flowers, which could undoubtedly provide bumblebee forage to some extent. However, the relatively short period of time during which these crops are in flower means that they are unlikely to meet the requirements of bumblebees throughout their season (Carvell *et al*. 2007). The queens of some species emerge from hibernation as early as February, whilst the colonies of other species are present right through into the late summer and early autumn (Goulson 2003a). Therefore, there is a lengthy time period throughout which forage plant material must be available in order to support a diversity of bumblebee species.

In order to reduce and reverse the adverse impact of agriculture on the environment, agri-environment schemes have been set up to encourage farmers and land owners to, amongst other things, restore arable land to wildflower rich habitat (Kells *et al*. 2001). Carvell *et al*. (2007) compare the efficacy of such agri-environment schemes in England designed specifically to enhance the abundance and diversity of bumblebees on arable field margins. They established that pollen and nectar rich mixes can rapidly improve field margins for bumblebees and their implementation is preferable to sowing margins with grass mixes, allowing natural regeneration of plant communities or managing margins as conservation headlands. For these schemes to be of any significant benefit to bumblebees it has been suggested that resources should be sown in several patches across the landscape and not just at a single location as this strategy is likely to support a greater number of bumblebee colonies (Dramstad *et al*. 2003). In order to encourage farmers to enhance field margins for bumblebees and other pollinating species it is important that pollen and nectar rich seed mixes can be sown and managed with standard farm equipment, are inexpensive and do not develop into a weed problem in adjacent arable crops (Carreck & Williams 2000).

Conservation strategies within the wider farmed landscape are important for increasing the provision of bumblebee forage plants and investigations into the benefits of mass flowering crops could prove useful in understanding how pollinators exploit commercial crops. However, the rate of decline of the UK's rarest bumblebee species is now such that they now only survive in pockets of semi-natural habitat which have suffered little agricultural disturbance. For these rare populations to persist, it is paramount that the correct conservation strategies are devised and implemented in their remaining strongholds (Carvell *et al*. 2007).

There is evidence to suggest that agri-environment schemes are able to provide resources for bumblebees in England (Carvell *et al*. 2007) but much is still lacking in terms of understanding the ecological requirements of the rarest bumblebee species (Goulson *et al*. 2006). Therefore, further research is required in order to establish how best to manage existing habitat for the rarest *Bombus* species, particularly in Scotland where, although existing agri-environment schemes may inadvertently provide some suitable foraging habitats (Lye *et al.* 2009), bumblebee specific agri-environment schemes are not currently available.

1.3 The great yellow bumblebee, *Bombus distinguendus*

Relatively little is known about the UK's rarest bumblebee species, the great yellow bumblebee, *Bombus distinguendus* (Goulson *et al*. 2006). The queens emerge from hibernation from mid May to early June and are, as their name would suggest, large and dusky, golden yellow in colour with a distinctive single black thoracic band (Sladen 1912; Benton 2006).

The species exhibits a northerly distribution across Europe and Asia (Benton 2006; Williams *et al*. 2007) and although never a common species, *B. distinguendus* was once widespread throughout much of the UK (figure 1.1a) (Sladen 1912; Williams 1982; Edwards 1997). The species has, like several of its *Bombus* counterparts, suffered a marked decline and range retraction in recent decades and the few remaining UK populations are now found only in the very northern and western fringes of Scotland (Benton 2006; NBN 2010). This species has become particularly associated with species-rich machair grassland, a habitat which is also a global rarity, limited in distribution to the North and West of Scotland and Western Ireland (Angus 2001; Edwards & Williams 2004; Goulson *et al*. 2006; JNCC 2010).

Bombus distinguendus has become noticeably distributed across a coastally based range but it is not believed to be a habitat specialist, despite its strong affiliation with machair (Goulson *et al.* 2006). The forage plants which are understood to be important for the species, include those typical of many semi-natural grassland habitats such as red clover (*Trifolium pratense*) and common knapweed (*Centaurea nigra*) (Edwards & Williams 2004; Benton 2006; Goulson *et al*. 2006; Charman 2007). It has been suggested that the coastal areas where this bumblebee currently persists have escaped much of the agricultural intensification which has been held accountable for its disappearance elsewhere in the UK (Goulson *et al*. 2006). Areas such as the Outer Hebrides and the North coast of Scotland, which have not undergone agricultural intensification to the same extent as the rest of the UK, continue to support *B. distinguendus* populations and indeed it appears to thrive in these regions. This is exemplified in North and South Uist where *B. distinguendus* and another of the rarer *Bombus* species, the moss carder bumblebee (*Bombus muscorum*), are comparatively common in relation to other bumblebee species (Darvill *et al*. 2010), although at present no permanent monitoring system is in place to confirm this.

The relative inaccessibility of coastal habitats has allowed semi-natural grasslands in these areas to remain intact due to the impracticality of intensively farming them. Therefore, the emphasis for conserving *B. distinguendus* and other rare *Bombus* species is largely directed at the conservation and restoration of wildflower-rich habitats (Edwards & Williams 2004).

1.3.1 Machair – The Last Stronghold

Machair is a low-lying calcareous plain which forms on soils derived from mineral sand and shell fragments that are blown inshore and deposited by prevailing winds (Angus 2001). The coastal 'machair system' as a whole encompasses a spectrum of habitat types ranging from the fore dunes adjacent to the sea shore, through to the grassland plains, machair lochs, fens and salt marshes and culminating in the black land where sand based soils graduate into peat rich moorland (Angus, 2001). The section of this diverse system which is of greatest importance to *B. distinguendus* and other bumblebee species is the floristically diverse machair grassland which lies immediately behind the dune system. However, the highly specific geographical location of machair, on the peripheral fringes of Scotland and Ireland, does not reflect the historic distribution of *B. distinguendus* (figure 1.1: a-b). This poses the question of why this bumblebee has disappeared from so many parts of the UK and is now ostensibly a machair specialist, when historically its range would have included Central Scotland, Central and Southern England (Edwards 1997; Goulson *et al*. 2006; NBN 2010).

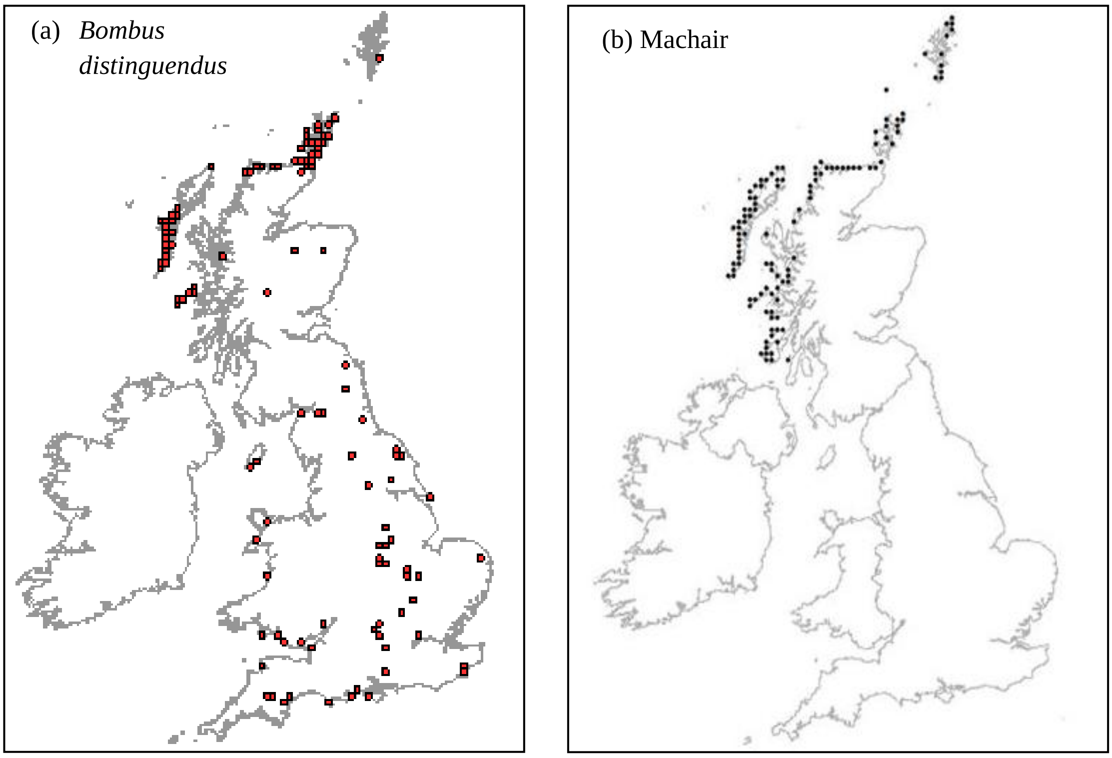

Figure 1.1 (a-b): (a) The historic UK distribution of the great yellow bumblebee, *Bombus distinguendus* (NBN Gateway) and (b) the distribution of machair habitats in the UK (JNCC 2010).

The spectacular floral displays, for which Hebridean machair is famous, are far from an entirely natural phenomenon. Machair has been inextricably linked with human culture for at least two thousand years, with evidence of anthropogenic activity in the form of low intensity agricultural practices dating back to Neolithic times (Ritchie 1967; Owen *et al*. 1996). Crofting is the most recent form of agriculture to take place on machair and this low intensity land use is believed to help maintain the species diversity of machair (Owen *et al*. 1996; Owen *et al*. 2001; Love 2003). Land management undoubtedly has an impact on plant communities (; Vickery *et al*. 2001; Tasser & Tappeiner 2002;

Cooper *et al*. 2005) and traditionally, Scottish machair has been subject to small scale cultivation and winter grazing (Love 2003; Gaynor 2006). Despite the sandy soils of machair grassland being the most suitable areas of the Hebridean Islands on which to grow crops, the soil is sufficiently deficient in organic matter, and nutrients including potassium and phosphorus, that prolonged successional cropping is not a viable option and hence the rotational nature of traditional machair related agriculture (Owen *et al*. 1996).

This rotational cultivation of the land creates a matrix of habitat types consisting of strips of cereal crop such as bere barley, black oats and rye interspersed with grazing pasture, fallow areas and lazy beds, the linear mounds created for potato production (Owen *et al*. 1996; Kent *et al*. 2005). The majority of the forage plants suitable for bumblebees occur in the fallow areas (Charman 2007) and these strips vary in maturity due to the rotational nature of machair cropping, ranging from one to five years in age. This traditional network of narrow strips of agricultural land can still be seen in parts of the Outer Hebrides, beautifully exemplified by some of the systems in South Uist (Angus 2001; Owen *et al*. 2001).

In contrast to the agricultural intensification which has taken place across much of the rest of the UK, low intensity crofting practices are a vital element in the maintenance of floristically diverse machair. Regrettably though, these practices are becoming increasingly difficult to uphold and some areas of machair are becoming degraded. The number of livestock on crofts, and particularly the number of sheep, has increased in recent decades. Although there is evidence to suggest that this trend is reversing

(Scottish Agricultural College 2008), traditional rotational cropping and winter grazing regimes are still frequently replaced by grazing of the in-bye and machair throughout the year (Hansom & Angus 2005; Osgathorpe *et al*. 2011). One major impact of overgrazing is that vegetation becomes destabilized and this, combined with the action of livestock hooves and high numbers of rabbit burrows, has lead to serious levels of soil erosion and sand-blow (Owen *et al*. 1996). Soil disturbance, to some degree, has a positive effect on the seed bank and the subsequent emergent vegetation (Owen *et al*. 2001) and in the case of traditional crofting, this disturbance would occur in the form of shallow ploughing and some livestock induced soil erosion. However, if this soil disturbance is either too deep or repetitive, as is the case with high stocking densities, the ground becomes poached and machair vegetation struggles to re-establish (Kent *et al*. 2005).

Prolonged grazing periods in conjunction with the use of inorganic fertilisers, affect the species diversity of semi-natural grassland plant communities by promoting the growth and proliferation of dominant plant species (Söderström *et al*. 2001). Studies conducted in Sweden have found a negative correlation between grazing intensity and the species richness of bumblebees and butterflies in semi-natural grasslands (Söderström *et al*. 2001). Grazing animals invariably preferentially graze flower heads, removing sources of bumblebee forage plant material and in the long term, repeated over grazing can also result in dramatic changes to the species diversity of the semi-natural grasslands. Therefore, machair that has been excessively grazed is unlikely to provide the floral composition required by *B. distinguendus* and other rare bumblebee species, either now or in the future, without intervention.

The botanical diversity of machair is under threat from both unsuitable livestock numbers and the use of nitrogenous fertilizers that significantly increase soil fertility. Heightened soil fertility can have a considerable impact on the composition of plant communities and subsequently is likely to have an indirect affect on the composition of the soil seed bank (Akinola *et al*. 1998; Kalamees & Zobel 2002). The seed bank can be defined as the population of viable seed buried in the soil and these viable seeds are most likely to be concentrated in the top 2-3cm of soil, although some seed may persist deeper in the soil for several decades (Leck *et al*. 1989). The soil seed bank is important for the conservation and restoration of plant communities and it is therefore important to understand how various management strategies affect the seed bank in comparison to the regular passage of time (Akinola *et al*. 1998).

Conversely to the issue of intensified methods, and perhaps of greater threat to the floristic diversity of machair, is the increasingly common abandonment of crofting. Under-grazing and lack of arable cultivation has become highly problematic in recent years as the viability of crofting as a sole income is now often unrealistic in the agriculturally competitive market (Kent *et al*. 2003). Many crofters are forced to reduce the use of time consuming traditional farming methods in order to allow them a second or third form of employment. However, if crofts do become abandoned and grazing is removed from the machair altogether, there are concerns that the species-rich grassland will become rank and species-poor (Owen *et al*. 1996; Kent *et al*. 2003).

1.3.2 Machair management and restoration: The future of great yellow bumblebee conservation?

Although machair has not always been the main stronghold for *B. distinguendus*, it has now become so and the agricultural changes taking place on machair pose a serious threat to the species (Edwards 1997). Therefore, it is imperative to manage this habitat effectively in order to ensure the survival of one of the UK's rarest invertebrates. There are populations of *B. distinguendus* which exist in parts of Scotland where machair does not, in the Orkney Isles for example, and so there is scope for creating species specific management prescriptions in these areas also. Improving the suitability of degraded machair as a habitat for this rare bumblebee will inevitably have a positive impact on a number of other species, improving and maintaining machair biodiversity as a whole.

1.4 Aim and structure of the thesis

This principle aim of this thesis is to develop a greater understanding of how machair habitats in northwest Scotland can be managed in order to deliver foraging resources for bumblebees, particularly the UK's rarest *Bombus* species *Bombus distinguendus*. In order to achieve this, the research presented here examines the influence of current crofting practices on the abundance of foraging bumblebees across North and West Scotland and combines this information with a detailed exploration of the machair seed bank and potential machair restoration treatments in the Scottish Hebrides.

Specifically this thesis addresses the following questions:

1) What are the current foraging habits of *Bombus distinguendus* in the UK, with particular reference to populations foraging on machair in the Outer Hebrides? (Chapter 2)
2) How do current crofting practices in northwest Scotland affect the abundance of bumblebees and their forage plants? (Chapter 3)
3) Do current schemes implemented in the Outer Hebrides to improve early cover habitat for corncrakes, provide foraging resources for bumblebees? (Chapter 4)
4) Does the seed bank of machair grassland have the potential to restore floral resources to degraded areas? (Chapter 5)
5) What are the most effective methods for restoring bumblebee foraging resources to machair which has lost floral diversity as a result of changes in agricultural practices? (Chapter 6)

Figure 1.2: The great yellow bumblebee, *Bombus distinguendus*

2 A comparative analysis of the foraging behaviour of the rare and declining bumblebee *Bombus distinguendus*

2.1 Abstract

The great yellow bumblebee, *Bombus distinguendus*, is the UK's rarest bumblebee species. The marked decline of this and other *Bombus* species in recent decades has been largely attributed to the widespread intensification of agriculture that has been experienced by much of Western Europe since the end of the Second World War. In order to gain a greater understanding of the foraging behaviour of *B. distinguendus*, we looked at the foraging habits of this species on machair grassland in the Outer Hebrides, Scotland. Machair, a rare coastal grassland habitat, has become strongly associated with remaining populations of this bumblebee and hence data collection focused primarily on these areas. However, in order to develop a broader understanding of *B. distinguendus'* foraging habits throughout its current UK range, foraging records collected from across the North and West of Scotland were collated and entered into an existing dataset compiled by Goulson *et al*. (2005), which examined the use of forage plant families by 16 *Bombus* species. This study demonstrates that *B. distinguendus* uses forage plant families similarly to other rare, long-tongued *Bombus* species and the workers of this species predominantly forage on members of the Asteraceae and Fabaceae family. We therefore recommend that future conservation measures for *B. distinguendus* in Scotland could reasonably be focused on the production and implementation of pollen and nectar mixes throughout its current range.

2.2 Introduction

Bombus distinguendus is a large and striking insect, distributed broadly across northern and central Europe and Asia. The species has suffered a significant decline and range retraction in recent decades as a result of agricultural intensification, becoming extinct in four of eleven European countries studied by Kosior *et al*. (2007). Historically found throughout the UK, *B. distinguendus* now persists only in the North and West of Scotland, predominantly in the Inner and Outer Hebrides, the Orkney Isles and the northern-most fringes of the Scottish mainland (Goulson 2003; Benton 2006; NBN 2010). The current UK distribution of this species is mirrored by the areas of Scotland that encompass machair grassland; a habitat that has become strongly associated with remaining *B. distinguendus* populations (Hughes 1998; Goulson 2003; Benton 2006; Charman 2007). However, it is worth noting that this species has previously occurred in areas where machair does not and therefore it is not considered to be a machair specialist (Goulson *et al*. 2006).

As the decline of bumblebees across the agricultural landscapes of Western Europe has become increasingly well recognised and documented, the development of seed mixes and agri-environment schemes designed to compensate for the loss of suitable foraging habitat has also increased (Kells *et al*. 2001; Carreck & Williams 2002; Carvell *et al*. 2004; Carvell *et al.* 2007). Research carried out in agricultural systems in England has demonstrated the importance of implementing bumblebee specific wildflower-rich seed mixes in order to conserve bumblebees within the wider agricultural landscape (Carvell *et al*. 2004). However, to date there has been a lack of similar research undertaken in Scottish systems. Lye *et al*. (2009) investigated the benefits of three Scottish agri-environment scheme options for foraging and nesting bumblebee queens. Although field margin habitats were found to provide emergent queens with foraging resources, none of the options examined were specifically targeted at bumblebees and the study focused on agricultural systems in Central and Eastern regions of Scotland, which do not support *B. distinguendus*.

The aim of this study was twofold: Firstly to understand the foraging behaviour of *B. distinguendus* across its current UK range, including the areas of machair grassland that arguably hold the largest remaining populations of *B. distinguendus*; and secondly to compare *B. distinguendus'* use of forage plant families with other UK *Bombus* species. Here we collect records of foraging *B. distinguendus* on machair, and combine these with records that have been accumulated from other studies of *B. distinguendus* undertaken throughout the species' current UK range (Dawson *unpublished data*; Charman 2007). This *B. distinguendus* data was then incorporated into an original data set compiled by Goulson *et al*. (2005), which includes more than five thousand foraging observations for 16 *Bombus* species. Goulson *et al*. collected records from across a number of sites in the UK and in New Zealand (included since all the species in New Zealand are of British origin and in New Zealand they forage almost exclusively on European plants). The authors argue that, to date, the majority of bumblebee ecology research has been focused on the widespread, ubiquitous *Bombus* species and studies that focus on the rare and declining species are required in order to inform the development of future bumblebee conservation strategies. Unfortunately *B. distinguendus* records were not included in their research so by incorporating the *B.distinguendus* records accumulated here with the extensive records for other *Bombus* species compiled by Goulson *et al*., this chapter aims to fill a gap in the existing research on bumblebee foraging ecology, by examining how *B. distinguendus* uses forage plant families in relation to other *Bombus* species.

2.3 Methods

2.3.1 Study sites

Bumblebee forage use was examined and quantified at 15 machair sites across the Outer Hebridean islands of Berneray, North Uist and South Uist between 30th July and 13th August 2009. These islands were selected because they demonstrate arguably some of the most florally rich examples of machair (Angus 2001) and hold what are probably the largest remaining UK populations of *B. distinguendus*. Individual machair sites were selected on the basis that they exhibited an abundance of mature machair vegetation suitable for foraging bumblebees and sites were situated a minimum of 1.5km apart from one another.

2.3.2 Bumblebee and vegetation surveys

Following the methodology outlined by Goulson and Darvill (2004), Goulson *et al.* (2005) and Goulson *et al*. (2008), each site consisted of an area with a radius of approximately 100m. These sites were then searched for one man hour, during warm dry weather conditions, between the hours of 08:00 and 18:00 and the total number of inflorescences within each search area was estimated, by eye, for each of the forage plant species present. All areas were searched systematically to avoid, as far as possible, recounting individual bees and all foraging bumblebees observed were recorded to species and caste level. The plant species on which bees were observed foraging was recorded and it was noted whether bees were collecting pollen or nectar. Bees were only recorded as collecting pollen if they were observed actively grooming pollen into their corbiculae.

2.3.3 Forage plant preferences

In order to examine the specific foraging preferences of *B. distinguendus*, observations of foraging workers and the relative abundance of forage plant species on machair were summed across all sites and examined using a preference index, as described by Kells *et al*. (2001).

$$\mathbf{PI = (V_{\mathit{k}} / V_{\mathit{t}}) / (A_{\mathit{k}} / A_{\mathit{t}})}$$

In this equation, V_k represents the number of foraging visits made by *B. distinguendus* to forage plant species *k*, V_t represents the total number of visits made by *B. distinguendus* to all available forage plant species, A_k represents the total number of available inflorescences of forage plant species *k* and A_t represents the total number of inflorescences of all forage plant species available.

2.3.4 Data analysis

Records of foraging *B.distinguendus* collected during this study were combined with existing records of *B. distinguendus* collected from across it Scottish range, (Dawson, *unpublished data;* Charman 2007) and incorporated into an original data set compiled by Goulson *et al*. (2005) as described in the introductory section of this chapter. Patterns of forage plant visitation by workers of different bumblebee species, including

B.distinguendus, were then examined using principal components analysis (PCA) on the proportion of foraging visits made to different plant families. PCA analysis was carried out in the software program R, version 2.10.1 (R Development Core Team 2009).

In their study, Goulson *et al*. (2005) analysed patterns of forage plant use by looking at pollen and nectar collecting records separately. Although some of the bees observed at the machair sites in this study had pollen in their pollen baskets and had obviously been collecting pollen, none of these bees were recorded actively brushing pollen grains into their corbiculae. Therefore, for the purposes of analysis, foraging visits were not separated into pollen and nectar collecting categories and all foraging visits were combined. Studies which have previously examined the foraging habits of *B. distinguendus* but which did not distinguish between the different castes were also collated and summarised in tabular form in order to allow a descriptive comparison of forage use by this species across a wider geographical area (table 2.1; Hughes 1998; Bridge 2007; Redpath *et al*. 2010).

2.4 Results

2.4.1 Bumblebees on machair

A total of 529 bumblebees, belonging to five different *Bombus* species were observed foraging on machair during this study (table 2.2). *Bombus muscorum* was the most frequently recorded species on machair, followed by *B. distinguendus*. There are three morphologically indistinguishable *Bombus* species found in the Western Isles, *B. lucorum*, *B. magnus* and *B. cryptarum;* observations of these species were grouped and recorded under the single category of *Bombus lucorum* (Waters *et al*. 2011). Only one *Bombus jonellus* was observed and so this species was removed from further analysis.

2.4.2 Forage plant use and forage preferences of bumblebees on machair

Foraging visits were made to 13 different plant species, although a total of 16 known forage plant species were observed across the various machair sites (table 2.2; Charman 2007; Redpath *et al*. 2010). The most abundant forage plant on machair during the survey period was common knapweed, *Centaurea nigra* (table 2.2). This was reflected by the high proportion of foraging visits made by each *Bombus* species to *C. nigra* (74%, 55%, 57% and 80% of foraging visits made by *B. distinguendus*, *B. muscorum*, *B. lucorum* and *B. hortorum* respectively). Red clover, *Trifolium pratense*, the sixth most abundant forage plant species on machair, was the second most commonly visited species and received 10% of all foraging visits (table 2.2). Combined with visits to *C. nigra*, these two species represent 69% of all bumblebee foraging visits observed, demonstrating that the most abundant floral resources are not necessarily the most frequently utilised by foraging bumblebees.

The specific foraging preferences of *B. distinguendus* workers on machair habitats also emphasised this point as the most abundant forage plant species were not necessarily the most frequently utilised. *B. distinguendus* exhibited the highest preference for spear thistle (*C. vulgare*) which was the least abundant of the ten most frequently recorded forage plant species (fig. 2.1; table 2.2). The remaining three species for which *B. distinguendus* workers showed greatest preference were *C. nigra*, *Vicia cracca* and *T. pratensis*, which belong to the Asteraceae and Fabaceae families (fig. 2.1). The forage plant preferences of male *B. distinguendus* were not calculated due to the relatively small number of males observed during this study (n=13).

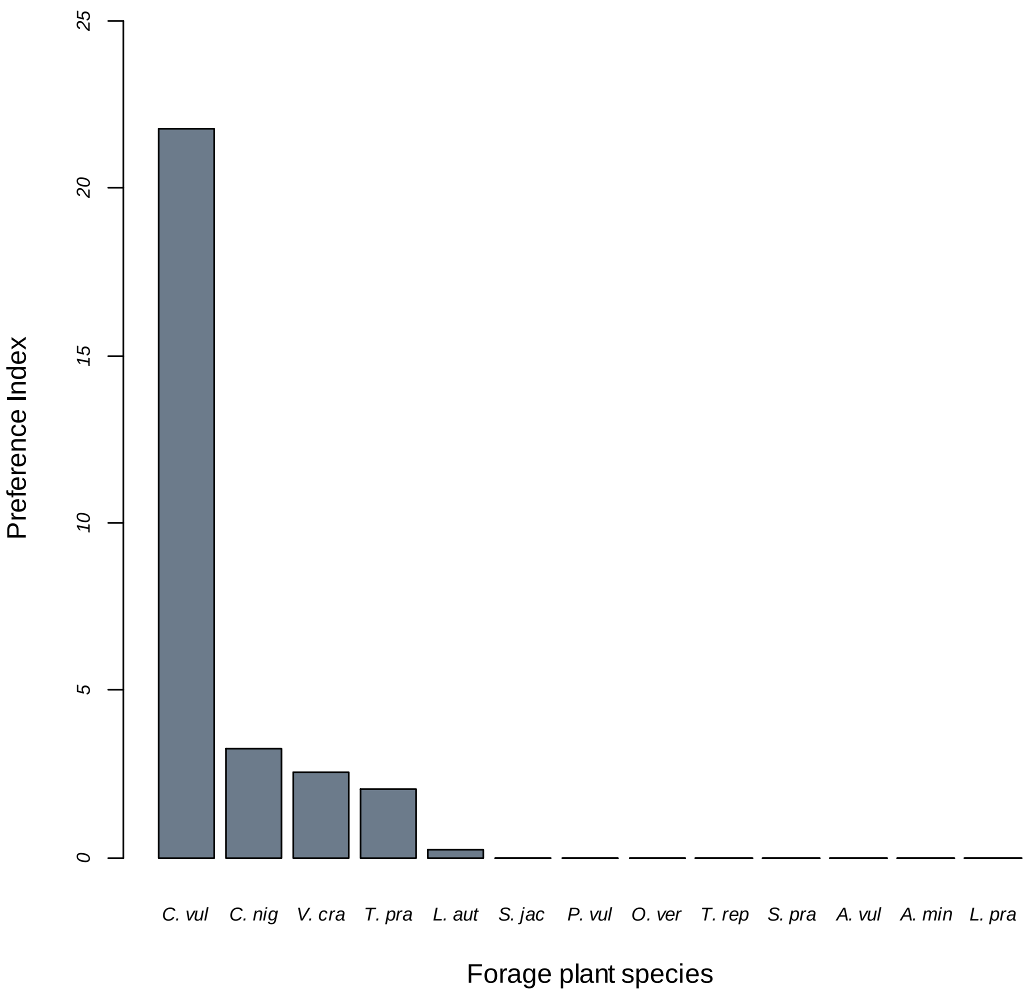

Figure 2.1: The preferences of *Bombus distinguendus* workers for each flower species present across 15 machair sites in the Outer Hebrides. C. vul = *Cirsium vulgare*, C. nig = *Centaurea nigra*, V. cra = *Vicia cracca*, T. pra = *Trifolium pratense*, L. aut = *Leontodon autumnalis*, S. jab = *Senecio jacobaea*, P. vul = *Prunella vulgaris*, O. ver = *Odontites verna*, T. rep = *Trifolium repens*, S. pra = *Succisa pratensis*, A. vul = *Anthyllis vulgare*, A. min = *Arctium minor* and L. pra = *Lathyrus pratensis*.

Table 2.1: A summary of all foraging records for *Bombus distinguendus* accumulated from across its current UK range. In addition to the data collected for this chapter, records have been collated from chapters 3 and 4 of this thesis and from Hughes 1998; Bridge 2007; Charman 2007 and Dawson *unpublished data* 2009. Information regarding the caste of foraging bumblebees was included where available.

Species	**All bees**	**Queens**	**Workers**	**Males**	**Caste unknown**	**Location**
Trifolium pratense	115	30	24		61	Berneray, Caithness, Coll, N. Uist, Orkney, S. Uist
Centaurea nigra	100	1	60	7	32	N. Uist, S. Uist
Trifolium repens	87	57	24		6	Coll, Caithness , Orkney, S. Uist
Vicia cracca	34	11	5		18	Berneray, Coll, N, Uist, Orkney, S. Uist
Rhinanthus minor	29	25			4	Coll, N. Uist, S. Uist
Cirsium vulgare	29	4	10	1	14	Caithness, Coll, N. Uist, Orkney, S. Uist
Phacelia tanacetifolia	26		4	2	20	Caithness , N. Uist, Orkney
Prunella vulgare	16	2	4		10	Coll, S. Uist
Senecio jacobaea	15		5		10	Coll, N. Uist, S. Uist
Stachys palustris	11	1	10			Caithness
Cirsium palustre	10	4			6	Caithness
Stachys sylvatica	9		6		3	Orkney
Galeopsis tetrahit	8				8	Orkney
Lathyrus pratensis	5	5				Caithness

Table 2.2: The number of bumblebees observed (all castes combined) across fifteen machair sites in the Outer Hebrides and the plant species on which they were observed foraging.

Family	**Species**	**Mean estimated no. of inflorescences per site (± 1 S.E)**	***B. distinguendus***	***B. muscorum***	***B. lucorum***	***B. hortorum***	**Total visits**
Asteraceae	*Leontodon autumnalis*	93627 ± 24174	3	45	3	0	51
Asteraceae	*Centurea nigra*	106059 ± 27384	58	213	35	4	310
Asteraceae	*Senecio jacobaea*	33960 ± 8768	2	15	15	0	32
Asteraceae	*Cirsium vulgare*	1109 ± 286	4	5	0	0	9
Asteraceae	*Arctium minus*	13 ± 3	0	6	3	0	9
Asteraceae	*Cirsium arvense*	7667 ± 1980	0	0	0	0	0
Dipsacaceae	*Succisa pratensis*	67 ± 17	0	3	0	0	3
Fabaceae	*Lathyrus pratensis*	3 ± 1	0	1	0	0	1
Fabaceae	*Trifolium pratense*	31407 ± 8109	10	43	0	1	54
Fabaceae	*Trifolium repens*	890 ± 230	0	7	0	0	7
Fabaceae	*Vicia cracca*	2787 ± 720	1	27	3	0	31
Fabaceae	*Anthyllis vulneraria*	15 ± 4	0	2	0	0	2
Lamiaceae	*Prunella vulgaris*	1341 ± 346	0	1	0	0	1
Scrophulariaceae	*Odontites verna*	95083 ± 24550	0	16	2	0	18
Scrophulariaceae	*Euphrasia officinalis*	90867 ± 23462	0	0	0	0	0
Scrophulariaceae	*Rhinanthus minor*	43 ± 11	0	0	0	0	0
	Total		**78**	**384**	**61**	**5**	**529**

2.4.3 The use of forage plants by Bombus distinguendus workers in relation to other Bombus species native to the UK

Of the foraging records compiled here, including those from the Goulson *et al*. (2005), more than 50% of foraging visits (pollen and nectar visits combined), across all *Bombus* species, were to plants from the Fabaceae. Plants from the Asteraceae and Boraginaceae families were the next most frequently visited with 10% and 12% of records to species from these families respectively. It is important to note that information regarding forage plant availability is not included here and so the results should be interpreted as observations of forage use within the areas that each species persists and are not therefore, indicative of the forage preferences of each species.

Principal components analysis summarised that 35.6% and 19.4% of the variation observed in the data could be explained by the first and second principal components respectively (fig. 2.2). The first of the two components depicted in figure 2.2 (Comp. 1) separates *Bombus* species according to their use of Fabaceae (negatively correlated) and Ericaceae (positively correlated). The two species most strongly associated with the use of Fabaceae are *Bombus lapidarius* and *B. hortorum* and the species most strongly associated with Ericaceae is *B. jonellus*. *Bombus distinguendus* was also associated with Fabaceae but not strongly so.

The second component (Comp. 2) separates *Bombus* species according to their use of Rosaceae and Scrophulariaceae (positively correlated) and Asteraceae and Lamiaceae (negatively correlated). *Bombus lucorum* and *B. hortorum* were the species most strongly associated with the use of the Rosaceae and Scrophulariaceae families and *B.*

lapidarius and *B. distinguendus* were most strongly associated with the use of plant species belonging to the Asteraceae and Lamiaceae families.

Figure 2.2 shows that although some species are more strongly associated with certain plant families, in general no clear patterns or clusters of *Bombus* species are observed. *B. distinguendus* is most closely clustered with *B. humilis*, *B. soroeensis* and *B. subterraneus* but only very loosely so. The use of different forage plant species by bumblebees is often described in relation to tongue length, with the longer tongued *Bombus* species tending to utilise plant species that have flowers with a deep corolla (Goulson 2003; Benton 2006). When examining pollen collecting records only, Goulson *et al*. (2005) found a significant positive correlation between principal component one and tongue length (Pearson's correlation) with longer tongued species specialising in plants from the Fabaceae. When similar analysis was undertaken here, with pollen and nectar collecting records combined, no such significant correlation was found between principal component one and tongue length (Pearson's correlation coefficient -0.28, p = 0.27), suggesting that there is no clear relationship between longer tongued bumblebee species and the use of forage plants from the Fabaceae family. However, in their paper, Goulson *et al.* (2005) go on to describe how principal components analysis on nectar-collecting records was less revealing than analysis on pollen-collecting records. It seems likely therefore, that by combining nectar and pollen collecting records the distinct pattern observed for pollen-collecting bumblebees is obscured to some extent, by the more scattered nectar-collecting records. Hence no clear groups are evident when analysing all foraging records combined (fig. 2.2).

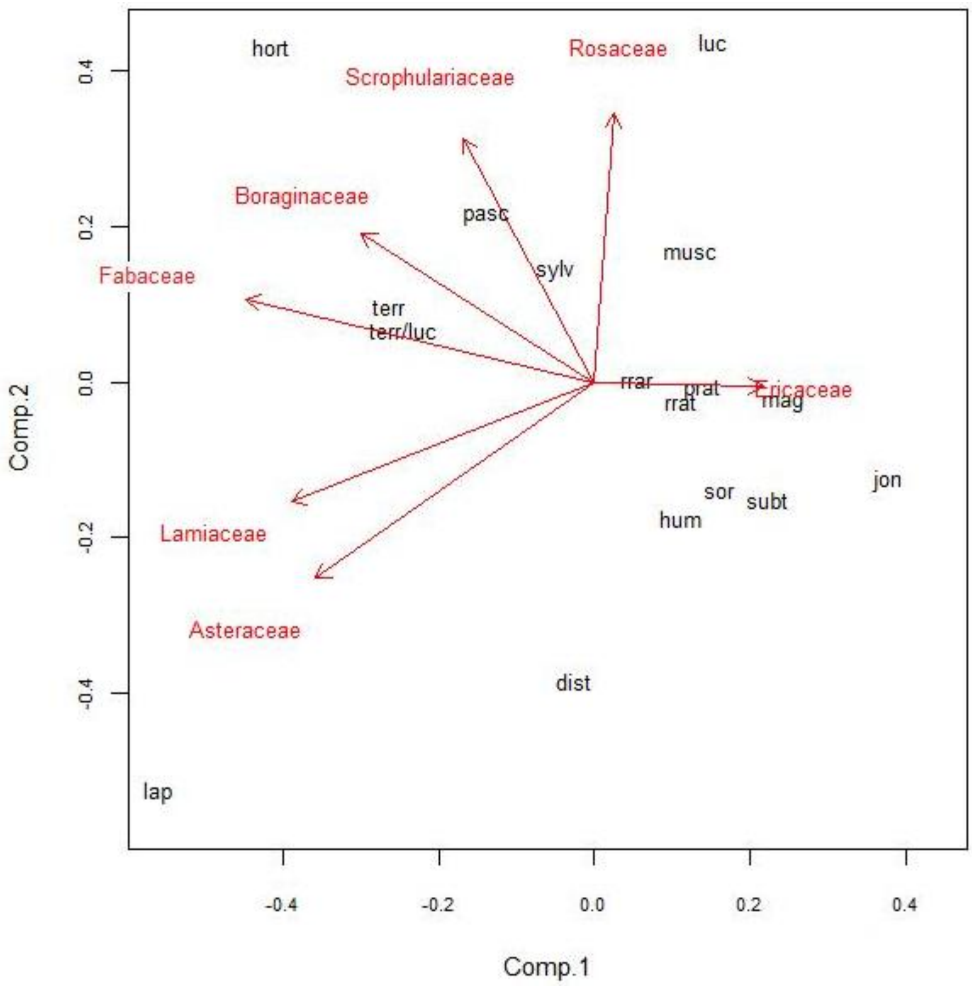

Figure 2.2: PCA biplot based on the proportion of visits to different plant families by foraging workers of 16 bumblebee species (nectar and pollen visits combined), collected from across the UK and New Zealand. The first two components account for 35.6% and 19.4% of the variation in forage use. Component 1 is negatively correlated with visits to Fabaceae and positively correlated with visits to Ericaceae. Component 2 is most positively correlated with visits to Rosaceae and Scrophulariaceae, and negatively correlated with visits to Asteraceae and Lamiaceae. dist = *B. distinguendus* (n=143), hort = *B. hortorum* (n=961), hum = *B. humilis* (n=152), jon = *B. jonellus* (n=257), lap = *B. lapidarius* (n=752), luc = *B. lucorum* (n=203), mag = *B. magnus* (n=144), musc = *B. muscorum* (n=495), pasc = *B. pascuorum* (n=429), prat = *B. pratorum* (n=93), rras = *B. ruderarius* (n=152), rrat = *B. ruderatus* (n=219), sor = *B. soroeensis* (n=59), subt = *B. subterraneus* (n=36), sylv = *B. sylvarum* (n=245), terr = *B. terrestris* (n=726). Terr/luc = *B. terrestris/B. lucorum* (n=605) was a category used at sites where both species occur and were indistinguishable from one another so observations were combined.

2.5 Discussion

The data presented here suggest that although no clear patterns of forage plant use were observed, *B. distinguendus* uses plant families in a similar way to a cluster of other rare, long-tongued species. Principal components analysis of worker bee forage use demonstrated that *Bombus humilis*, *Bombus soroeensis* and *Bombus subterraneous* (the latter now extinct in the UK) were loosely clustered with *B. distinguendus,* indicating that the greatest proportion of their foraging visits were to plant species from the Lamiaceae and Asteraceae families. However, *B.distinguendus* was more noticeably associated with plants from the Fabaceae family than these other rare bumblebee species (fig. 2.2). It is worth noting that after the addition of the *B. distinguendus* data to the original data set from Goulson *et al*. (2005), principle component one remained strongly correlated with Fabaceae. Goulson *et al*. (2008b) also found a similar relationship when examining the diet breath and rarity of bumblebees in Polish systems.

To date, research which has investigated the foraging requirements of *B. distinguendus* populations in the UK has focused on small, specific regions and attempts to examine the use of forage plants across the entirety of its Scottish range are limited (Hughes 1998; Bridge 2007; Charman 2007). Here, existing records of *B. distinguendus* collected from across Scotland have been compiled in order to provide a detailed overview of how this species uses forage plants (table 2.1). Observations of *B. distinguendus* collected during this study have demonstrated the importance of *C. nigra* and the preference indices calculated revealed that *B. distinguendus* workers showed a strong preference for *C. vulgare* both of which belong to the Asteraceae family. However, observations compiled from across Scotland have shown that of the four most commonly utilized forage plants, three (T. *pratense*, *V. cracca* and *T. repens*) are from the Fabaceae family. This information concurs with a large number of studies which highlight the importance of the Fabaceae family, and *T. pratense* in particular, as key forage plants for many bumblebee species (Bäckman & Tiainen 2002; Mänd *et al*. 2002; Goulson & Darvill 2004; Goulson *et al*. 2005; Diekötter *et al*. 2006; Goulson *et al*. 2006; Charman, 2007; Goulson *et al*. 2008a; Goulson *et al.* 2008b).

Interestingly, the PCA analysis presented here suggests that *B. distinguendus* although certainly associated with the use of forage plants from the Fabaceae family, is most strongly associated with plants from the Asteraceae family. The majority of foraging records of *B. distinguendus* collated here were collected during the month of August when worker numbers are likely to be at their highest. This is also when plants from the Asteraceae, and particularly *C. nigra* and *C. vulgare*, are at their most abundant on Scottish machair systems (N. Redpath Pers. Obs.). This could go some way in explaining why species from this plant family are most frequently used by *B. distinguendus*. To gain a more comprehensive impression of forage plant family use, future studies should incorporate records of foraging *B. distinguendus* collected throughout the colony's lifecycle (June through to September). Records for the other species described in the Goulson *et al*. (2005) dataset were collected between June and August (UK records) and hence are likely to be more representative of the dietary repertoire of each species than was collected for *B. distinguendus* here.

An aspect of bumblebee foraging ecology that was not analysed here was the use of different plant families for the specific collection of pollen and nectar. Pollen-collecting records gathered here were too few to analyse separately as has been done in some studies, but other long-tongued and related bee species such as *B. subterraneus* are known to collect much of their pollen from Fabaceae (which provides unusually protein-rich pollen, Hanley *et al*. 2008), and we suspect that this is the case for *B. distinguendus.* It is interesting to note that bumblebee species are known to vary in their propensity for collecting pollen versus nectar, although this has never been adequately explained (Prys-Jones & Corbet 1991). Our data suggest that *B. distinguendus* is one of the species which make relatively few pollen-collecting visits but in order to confirm whether *B. distinguendus* truly uses forage plant families in a similar manner to other rare, long tongued *Bombus* species, more extensive pollen-collecting records would need to be obtained for this species and analysed separately as was done in Goulson *et al*. (2005).

Although the PCA analysis on forage plant use outlined here has not revealed a strong similarity between *B. distinguendus* and other *Bombus* species, by compiling foraging records from a range of sites this chapter has provided us with the most detailed list available of forage plant use by *B. distinguendus* (table 2.1). It reveals that queens appear to depend heavily on *Rhinanthus minor* and *Trifolium repens*, which are among the first species to flower on machair. Records for males are scarce, but suggest that they exhibit a preference for species from the Asteraceae family such as *C. nigra* and *C. vulgare* which is typical for male bumblebees of a broad range of species (Goulson *et al*. 2005). It is particularly striking that approximately 80% of foraging records across *B. distinguendus'* current UK range, summarised here, are to just six plant species, all of them widespread and associated with flower-rich grasslands. Therefore, similarly to other declining bumblebee species studied to date, *B. distinguendus* is clearly not rare because it has highly specialized dietary requirements or because it depends on rare plant species. Simple pollen and nectar mixes, including those which are available under agri-environment schemes, can readily provide these flowers, and provide a tool for conserving both this and many other rare bumblebee species (Carvell *et al*. 2004; Carvell *et al*. 2007; Potts *et al*. 2009; Williams & Osborne 2009).

3 Crofting and bumblebee conservation: The impact of land management practices on bumblebee populations in northwest Scotland

This chapter is based on the following paper;

Redpath, N., Osgathorpe, L.M., Park, K. & Goulson, D. (2010) Crofting and bumblebee conservation: The impact of land management practices on bumblebee populations in northwest Scotland. *Biological Conservation* 143: 492-500.

This paper was produced in collaboration with fellow PhD student, Lynne Osgathorpe at the University of Stirling. Lynne and I contributed equally to the experimental design, fieldwork, statistical analysis and production of the final manuscript. Consequently we are represented as joint first authors on the published paper.

3.1 Abstract

The northwest of Scotland is a stronghold for two of the UK's rarest bumblebee species, *Bombus distinguendus* and *Bombus muscorum*. The predominant form of agricultural land management in this region is crofting, a system specific to Scotland in which small agricultural units (crofts) traditionally operate low intensity cropping and grazing regimes. Crofting is considered to be beneficial to a wide range of flora and fauna. However, currently there is a lack of quantitative evidence to support this view with regard to bumblebee populations. In this study we assessed the effect of land management on the abundance of foraging bumblebees and the availability of

bumblebee forage plants across crofts in northwest Scotland. The results of our study show that current crofting practices do not support high densities of foraging bumblebees. Traditional crofting practice was to move livestock to uplands in the summer, but this has been largely abandoned. Summer sheep grazing of lowland pasture had a strong negative impact on bumblebee abundance and forage plant availability throughout the survey period. The use of specific 'bird and bee' conservation seed mixes appears to improve forage availability within the crofted landscape, although the number of bees observed remained low. Of the forage plants available, the three most frequently visited species were from the Fabaceae. We therefore conclude that the creation of agri-environment schemes which promote the use of Fabaceae-rich seed mixes and encourage the removal of sheep grazing on lowland areas throughout the summer are essential in order to conserve bumblebee populations within crofted areas.

3.2 Introduction

Farming is the predominant land use in much of Western Europe. In the UK, agricultural holdings spanned more than 17.3 million hectares in 2007, equivalent to 77% of the total landmass (DEFRA 2007). Intensification of agricultural practices in Western Europe reached its peak in the latter half of the 20th century (Robinson & Sutherland 2002), leading to a widespread reduction in landscape heterogeneity and a loss of many semi-natural habitats from farmed areas (Green 1990; Chamberlain *et al*. 2000; Robinson & Sutherland 2002). This is exemplified by the reduction in the area of unimproved lowland grassland in the UK, which declined by more than 90% between 1932 and 1984 (Fuller 1987).

Habitat loss through agricultural intensification has led to extensive declines in biodiversity throughout the UK and Western Europe (Green 1990; Chamberlain *et al*. 2000). In particular, population declines in a number of bumblebee (*Bombus*) species have primarily been attributed to the reduced availability of suitable foraging resources within the farmed landscape (Goulson 2003a; Carvell *et al*. 2006; Goulson *et al*. 2008a). A reduction in nesting and hibernation sites (Goulson 2003a; Goulson *et al*. 2008a), competition from introduced species (Goulson 2003b) and potential pathogen spillover from commercially reared colonies (Colla *et al*. 2006) have also been identified as possible contributing factors to the decline of bumblebees.

Three of the 25 British bumblebee species are now extinct (Benton 2006) and the rarest of the remaining species persist only in small isolated pockets which have largely escaped agricultural intensification (Goulson *et al*. 2006). The most north westerly fringes of Scotland are now considered to be an important stronghold for two of the UK's rarest bumblebee species, *Bombus distinguendus* and *Bombus muscorum* (Goulson *et al*. 2005; Benton 2006). Maintaining appropriate management in these remote areas is vital if these species are to persist in the UK. Typically, agricultural units in these areas are called crofts, a term used to describe a small area of enclosed land (Stewart 2005), although crofters also have rights to communal grazing areas. Crofting practices exist only in certain parts of Scotland known as the 'crofting counties' and these include the former counties of Caithness, Sutherland, Orkney, Shetland, the Outer Hebrides, Skye and the Small Isles, Argyll, Ross and Cromarty and Inverness (Stewart 2005). Within these counties, crofts are clustered together forming villages or crofting townships in which crofters implement small scale rotational cropping regimes alongside livestock production. Traditionally cattle and sheep graze the hills and moorland adjacent to the townships in the summer and lowland grasslands are grazed during the winter (Hance 1952; Moisley 1962; Caird 1987; Love 2003). These cropping and grazing regimes, combined with a limited use of artificial fertilisers and pesticides, renders crofting a very low intensity form of agriculture.

Crofted areas create a mosaic of habitats. Multiple small units in a township operate a range of land management practices on a small scale, including the implementation of fallow areas, a practice which is now often redundant elsewhere as artificial fertilisers remove the need to 'rest' nutrient poor soil. A mosaic of habitats is understood to promote high biodiversity and abundance within the agricultural landscape. Hence, crofting supports significant populations of a number of species which have declined elsewhere in the UK; for example corn bunting (*Miliaria calandra*) and corncrake (*Crex crex*) (Stroud 1998; Love 2003; Mackenzie 2007). However, crofting communities are changing. In the Western Isles of Scotland, the declining population size combined with an ageing population as a result of high outward migration of the young (Mackenzie 2007; Western Isles Council 2009), increasing house prices (Mackenzie 2007), changes in agricultural subsidies and the Crofting Reform Act (2007) are all leading to changes in the way crofts are managed.

At present there is a lack of quantitative information with which to assess the influence of different croft management practices on biodiversity. This chapter examines how land management practices currently implemented on crofts influence the abundance of foraging bumblebees and the availability of their key forage plant species. In order to conserve rare bumblebee populations within crofted regions it is necessary to identify land management practices which are of benefit to foraging bumblebees. The results of this study are intended to reduce the gaps in our knowledge regarding bumblebee populations within low intensity agricultural systems in the UK, and thereby inform future conservation strategies within these areas.

3.3 Methods

3.3.1 Study sites

Fieldwork was carried out on 31 crofts at four locations in northwest Scotland: Lewis, Harris, the Uists (considered as one study area as differences in crofting practices between North and South Uist were negligible in the context of this study), and Durness. A total of 10 crofters were responsible for the management of the 31 croft units surveyed. The land within each croft was subdivided into sections according to the management type implemented. In most cases a section was equivalent to a field. Each croft consisted of between 1 and 7 sections and the area of these sections ranged from less than 1 ha to a maximum of 5 ha. The land management type classifications used and their definitions are listed in table 3.1. Most crofters employed a subset (1-7) of these management types.

3.3.2 Bumblebee sampling methods

Each croft was surveyed for bumblebees three times between 5th June and 22nd August 2008. Each croft was surveyed once in each of the three months with the exception of July when restricted access to crofts managed by one of the ten crofters meant that only 27 of the 31 crofts were surveyed. Surveys were conducted along a zigzag transect line established in each section of the croft. The transect line looped across sections at 25m intervals in order to ensure that a representative area of each section was surveyed and that the incidence of multiple recording of individual bumblebees would be minimised. The bumblebee surveying methodology used here was adapted from the standard butterfly recording protocol developed by Pollard (1977). All actively foraging bumblebees observed within 2 meters on either side of the transect line were recorded and identified to species level. In addition, the plant species on which bumblebees were foraging were also recorded. In sections containing arable crops, which could not be accessed, the zigzag transect was replaced by an 'L' shaped transect along two adjacent perimeter edges and all bumblebees foraging within 2 meters of the crop side of the transect line recorded as before. Surveys took place in dry weather and when temperatures exceeded 12 °C. The number and species of livestock present within a section was also recorded.

Table 3.1: Land management types and their definitions, including the area of each management type surveyed.

Management	Definition	Transect area surveyed (m^2)
Arable	Cultivated land sown with an annual crop, including mixed cereals (barley, oats & rye) and root vegetables	160 - 600
Bird & Bumblebee Conservation Mix	A brassica-rich mix sown primarily to benefit a number of bird species and also foraging bumblebees. Contains kale, mustard, phacelia, fodder radish, linseed & red clover	200 - 2000
Fallow	Cultivated land that has not been seeded for one or more years	600 - 4200
Mixed Grazing	Land grazed throughout the year by a combination of both cattle and sheep	800 - 4600
Sheep Grazed	Land grazed at various times throughout the year by sheep	800 - 7000
Silage	A grass crop taken from semi-improved grassland, harvested whilst green and then partially fermented and used for livestock fodder	600 - 4600
Unmanaged Pasture	Formerly grazed pasture where active management has ceased	1200 - 3600
Winter Grazed Pasture	Pasture grazed between September and May	1600 - 6000

3.3.3 Forage plant sampling methods

The availability of bumblebee forage plants was recorded by carrying out vegetation surveys on all croft sections. A 0.5 x 0.5m quadrat was positioned every 50 meters along each of the bumblebee transects and all inflorescences present were counted and identified to species level. In arable sections quadrats were placed every 20 meters along the bumblebee transect as zigzag transect walks could not be performed. This allowed more representative sampling of this management type. Quadrats were placed within the crop, but in order to reduce crop damage these were sampled from the edge of the field; therefore, they may not necessarily be representative of the whole crop area. Vegetation surveys were repeated once in June, July and August so that the availability of bumblebee foraging resources on each management type could be quantified throughout the bumblebee flight period.

3.3.4 Data analysis

The effect of land management on bumblebee abundance was examined using generalised linear models (GLM) with quasi-poisson errors in the software package R version 2.7.2. Management type and crofter were included in the models as factors and transect area was used as an offset to account for the differences in the total area of each management type. For some sections, management changed over the three months of the study, so a separate model was constructed for each month of the survey period and an R^2 value was calculated to assess the fit of each model to the observed data. Where management was significant ($p< 0.05$), pair-wise post-hoc comparisons were conducted to assess differences in bumblebee abundance between management types. In addition to management type, the influence of sheep grazing on bumblebee abundance was specifically examined by categorising each croft section into either ‘sheep present’ or ‘sheep absent’ and performing a Mann-Whitney U test.

The availability of forage plants in each month was examined using generalised linear models in the same way as described above. The effect of croft management type was examined in relation to the mean number of bumblebee forage plant inflorescences per quadrat per section. Analyses were restricted to known bumblebee forage plants (table 3.2; Charman 2007), and included any additional species on which we observed bumblebees foraging. The relationship between bumblebee abundance and bumblebee forage availability was analysed using generalised linear models with quasi-poisson errors and included crofter as a factor and transect area as an offset.

Table 3.2: The proportion of visits made by foraging bumblebees to key forage plant species throughout the survey period.

		% Total Bumblebees		
Flower Species	**Family**	**June**	**July**	**August**
Trifolium repens	Fabaceae	49.2	33.3	8.0
Trifolium pratense	Fabaceae	1.7	13.3	15.9
Lotus corniculatus	Fabaceae	5.1	0	0
Vicia cracca	Fabaceae	1.7	13.3	11.6
Vicia sepium	Fabaceae	1.7	0	0
Lathyris pratensis	Fabaceae	0	4.4	0.7
Cirsium vulgare	Asteraceae	1.7	0	4.3
Cirsium arvense	Asteraceae	0	0	1.4
Centaurea nigra	Asteraceae	0	0	13.0
Leontodon spp.	Asteraceae	0	0	6.5
Hypochaeris glabra	Asteraceae	0	0	1.4
Rhinanthus minor	Scrophulariaceae	30.5	11.1	5.8
Pedicularis sylvatica	Scrophulariaceae	1.7	4.4	1.4
Odontites verna	Scrophulariaceae	0	8.9	3.6
Euphrasia officinalis	Scrophulariaceae	0	0	0.7
Prunella vulgaris	Labiatae	0	11.1	2.2
Lamium purpureum	Lamiaceae	0	0	0.7
Lamium amplexicaule	Lamiaceae	0	0	6.5
Brassica spp.	Brassicaceae	6.8	0	5.1
Succisa pratensis	Dipsacaceae	0	0.1	8.7
Filipendula ulmaria	Rosaceae	0	<0.1	0.7
Phacelia spp.	Boraginaceae	0	<0.1	0.7
Lychnis flos-cuculi	Caryophyllaceae	0	<0.1	0.7

3.4 Results

3.4.1 Bumblebee species

A total of 246 foraging bumblebees belonging to six species were recorded on crofts throughout the survey period (table 3.3). *Bombus muscorum* was the most commonly recorded species across the study area. *Bombus lucorum* was recorded less frequently but remained relatively common compared with *Bombus hortorum* and *B. distinguendus* which were both scarce. *Bombus jonellus* was not recorded on any crofts, although it does occur in the study areas.

Table 3.3: The percentage of each bumblebee species (total n = 246) observed foraging on crofts across the study area.

Bumblebee Species	% Total Bumblebees
*B. muscorum/pascuorum**	77.2
*B. lucorum/terrestris**	19.5
B. hortorum	2.4
B. distinguendus	0.8
B. jonellus	0.0

[*] *B. pascuorum* and *B. terrestris* were not present in the Outer Hebrides but due to the difficulty in distinguishing them from *B. muscorum* and *B. lucorum* respectively, these species were combined at Durness.

The bumblebee species recorded varied between study areas. Geographic location governed the species present on some sites, such as the ‘mainland ubiquitous’ species

Bombus terrestris and *Bombus pascuorum* (Benton 2006) which were only observed at Durness. Whilst the ranges of the remaining species extend across the study area (Benton 2006), *B. distinguendus* was only recorded on North Uist crofts and *B. hortorum* was absent from crofts on Harris.

There were seasonal variations in the abundance of bumblebees (fig. 3.1a-c), and these patterns were consistent across species. Abundance was highest in August when 58% of all bees were observed (<0.003 bees m^{-2} in June & July, <0.03 bees m^{-2} in August). Notably, *B. hortorum* increased fivefold in numbers between June and August.

3.4.2 Croft management and bumblebee abundance

Bumblebee abundance was consistently low on all croft management types across all three months. This was demonstrated by a total of 246 bumblebees counted across a three month period compared with Carvell (2002) who observed 475 bumblebees on Salisbury Plain over a much shorter period (five weeks). In addition, surveys on the southern Hebridean island of Oronsay, which also took place in the summer 2008, found 283 bumblebees within three weeks (N. Redpath *unpublished data*).

Despite low overall numbers, land management type did have a significant effect on bumblebee abundance in all months (table 3.4). The effect of crofter on bumblebee abundance was significant in July and August only (table 3.4). These models explained 22%, 70% and 47% of the variance in bee numbers in June, July and August respectively.

Table 3.4: A summary of test statistics derived from the model examining the effect of land management type and crofter on bumblebee abundance and on the abundance of bumblebee forage plant inflorescences across the survey period (*p = 0.05, ** p = 0.01, *** p = <0.001).

	Bumblebee abundance		**Floral abundance**	
Month	Management	Crofter	Management	Crofter
June	χ^2_7 = 18.24***	χ^2_9 = 13.00	χ^2_7 = 25.14***	χ^2_9 = 13.00***
July	χ^2_7 = 109.74***	χ^2_8 = 69.13***	χ^2_7 = 17.82*	χ^2_8 = 10.24
August	χ^2_7 = 71.76***	χ^2_9 = 41.444	χ^2_7 = 5.56	χ^2_9 = 31.56***

The utilization of each management type by foraging bumblebees varied between months (figs. 3.1a-c). Bumblebee abundance was low in June with little variation observed between management types (fig. 3.1a, table 3.5). However, significantly more bumblebees were observed on sections sown with 'bird and bee' conservation seed mixes or managed for silage than either sheep grazed sections or winter pasture. Using the median number of bees observed, 'bird and bee' conservation mix and silage sections supported 47 and 27 times as many foraging bumblebees respectively than sheep grazed areas. The differences in abundance remained relatively large between the 'bird & bee' conservation mix and silage sections when compared to winter grazed sections, with 16 and nine times as many bumblebees supported by these two management types respectively in June.

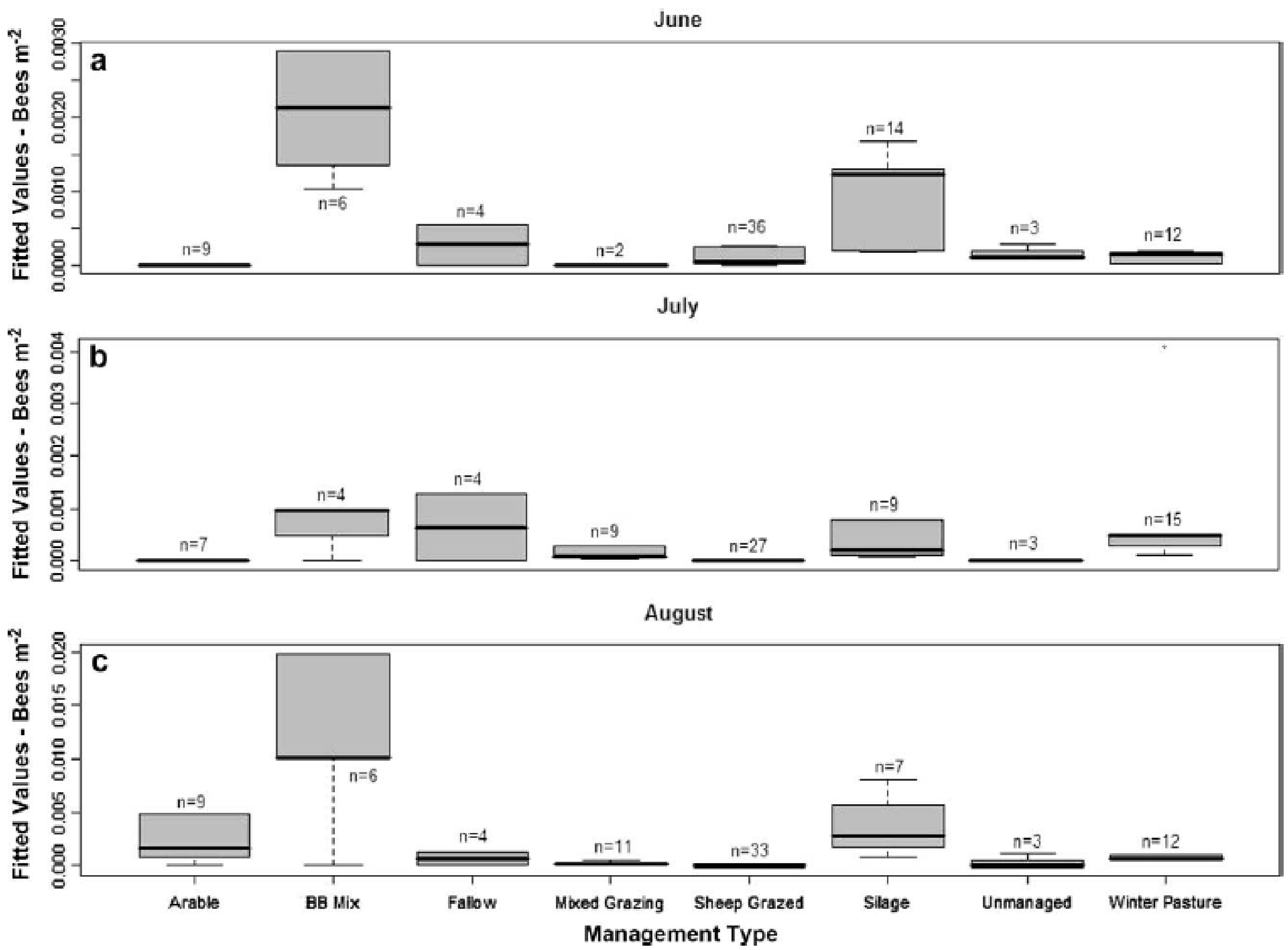

Figure 3.1a-c: Box plots showing fitted values from the models for bumblebee abundance across eight different croft management types in June, July and August respectively. Boxes represent the location of the middle 50 percent of the data and the whiskers indicate the inter-quartile range of the data.

Table 3.5: The effect of management type on bumblebee abundance in June. The t and p values are derived from pair-wise comparisons made between each of the management types, where the relationship is significant the values have been highlighted in bold. Negative t values show that the management types listed along the rows of the table are worse for bumblebees than the management listed as the column heading, and vice versa (**p* = 0.05, ** *p* = 0.01, *** *p* = <0.001).

Management Types	**Arable**		**B & B Mix** [a]		**Fallow**		**Silage**		**Sheep Grazed**		**Mixed Grazing**		**Unmanaged Pasture**	
	t	p	t	p	t	p	t	p	t	p	t	p	t	p
B & B Mix [a]	0.006	1.00												
Fallow	0.005	1.00	-1.500	0.14										
Silage	0.005	1.00	-1.263	0.21	0.773	0.44								
Sheep Grazed	0.005	1.00	**-2.559**	*****	-0.767	0.45	**-2.187**	*****						
Mixed Grazing	-<0.001	1.00	-0.002	1.00	-0.002	1.00	-0.002	1.00	-0.002	1.00				
Unmanaged Pasture	0.005	1.00	-1.228	0.22	0.195	0.85	-0.162	0.87	0.675	0.50	0.002	1.00		
Winter Pasture	0.005	1.00	**-2.403**	*****	-0.874	0.39	**-2.057**	*****	-0.270	0.79	0.002	1.00	-0.740	0.46

[a] B & B Mix refers to the Bird and Bumblebee Conservation Mix

In July, mixed grazing sections contained significantly fewer bumblebees than fallow, silage and winter pasture (fig. 3.1b, table 3.6). The greatest difference in abundance was found between fallow and mixed grazed sections, with fallow supporting nine times the number of bumblebees than mixed grazed sections. Silage and winter grazed pasture were three and six times better for foraging bees than mixed grazed sections.

Significant differences between management types occurred more frequently in August than in either June or July (fig. 3.1c, table 3.7). 'Bird and bee' conservation sections supported significantly more bumblebees than all other management types except unmanaged pasture in this month. The difference in the median number of bees was greatest between the 'bird & bee' conservation mix and sheep grazed sections, the 'bird & bee' mix supporting a remarkable 248 times more bumblebees than sections grazed throughout the year by sheep. Mixed grazed sections also supported much lower numbers of foraging bumblebees than the 'bird and bee' mix with 65 times fewer bees found on this management type. Differences in the median bumblebee densities for the remaining management types were much lower and ranged from four to 16 times fewer bumblebees on these sections compared to the 'bird & bee' conservation seed mix.

Sheep grazed sections supported significantly fewer bumblebees than all other management types except mixed grazing and fallow (table 3.7). The median number of bumblebees supported by mixed grazing and fallow was 4 and 16 times greater than that of sheep grazed sections (fig 3.1c). In addition to the differences between sheep grazed and 'bird & bee' conservation mix sections, silage and arable sections also maintained a much greater density of bumblebees than sheep grazed areas (68 and 41 times as many bumblebees respectively).

Sheep grazing had a negative effect on bumblebee abundance throughout the summer (fig. 3.2). There were significantly fewer foraging bumblebees observed on croft sections used for sheep grazing at any point during the survey period compared with all other sections (June: w = 2182.0, p = 0.02; July: w = 1782.5, p = 0.006; August: w = 2126.0, p =<0.0001).

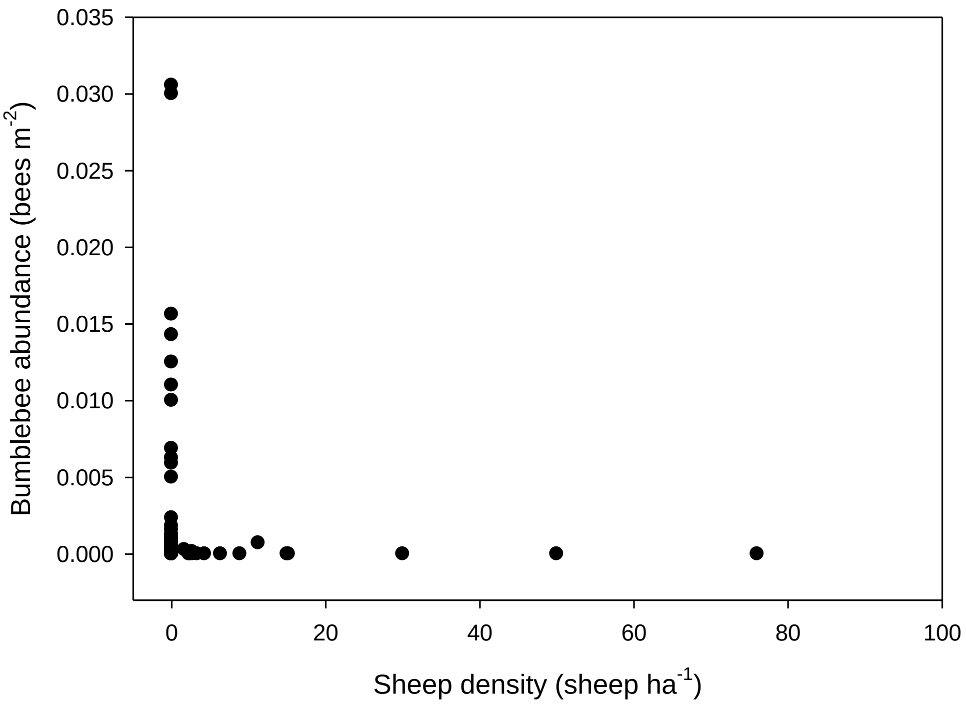

Figure 3.2: The relationship between the density of grazing sheep and the relative abundance of foraging bumblebees on crofts in August. The pattern was identical for June and July.

Table 3.6: The effect of management type on bumblebee abundance in July. The t and p values are derived from pair-wise comparisons made between each of the management types, where the relationship is significant the values have been highlighted in bold. Negative t values show that the management types listed along the rows of the table are worse for bumblebees than the management listed as the column heading, and vice versa (*p = 0.05, ** p = 0.01, *** p = <0.001).

Management Types	Arable		B & B Mix [a]		Fallow		Silage		Sheep Grazed		Mixed Grazing		Unmanaged Pasture	
	t	p	t	p	t	p	t	p	t	P	t	p	t	p
B & B Mix [a]	0.003	1.00												
Fallow	0.003	1.00	<0.001	1.00										
Silage	0.003	1.00	<0.001	1.00	-1.124	0.27								
Sheep Grazed	<-0.001	1.00	-0.005	1.00	-0.006	1.00	-0.006	1.00						
Mixed Grazing	0.003	1.00	<0.001	1.00	**-2.881**	**	**-2.018**	*	0.005	1.00				
Unmanaged Pasture	<-0.001	1.00	-0.002	1.00	-0.002	1.00	-0.002	1.00	1.44×10^{-6}	1.00	-0.002	1.00		
Winter Pasture	0.003	1.00	<0.001	1.00	-0.466	0.64	0.550	0.58	4.00×10^{-3}	1.00	**2.343**	*	0.002	1.00

[a] B & B Mix refers to the Bird and Bumblebee Conservation Mix

Table 3.7: The effect of management type on bumblebee abundance in August. The t and p values are derived from pair-wise comparisons made between each of the management types, where the relationship is significant the values have been highlighted in bold. Negative t values show that the management types listed along the rows of the table are worse for bumblebees than the management listed as the column heading, and vice versa (*p = 0.05, ** p = 0.01, *** p = <0.001).

Management Types	**Arable**		**B & B Mix** [a]		**Fallow**		**Silage**		**Sheep Grazed**		**Mixed Grazing**		**Unmanaged Pasture**	
	t	p	t	p	t	p	t	p	t	p	T	p	t	p
B & B Mix [a]	**3.298**	**												
Fallow	-1.792	0.08	**-4.463**	***										
Silage	0.892	0.38	**-3.727**	***	**2.677**	**								
Sheep Grazed	**-3.281**	**	**-5.596**	***	-1.842	0.07	**-4.104**	***						
Mixed Grazing	**-2.824**	**	**-5.380**	***	-1.069	0.29	**-3.845**	***	0.963	0.34				
Unmanaged Pasture	0.205	0.84	-1.875	0.07	1.116	0.27	-0.182	0.86	**2.311**	*	1.744	0.09		
Winter Pasture	-1.152	0.25	**-4.535**	***	0.825	0.41	**-2.507**	*	**2.897**	**	**2.187**	*	-0.743	0.46

[a] B & B Mix refers to the Bird and Bumblebee Conservation Mix

3.4.3 Croft management and forage plant availability

The relationship between the availability of bumblebee forage plants and management type throughout the survey period broadly paralleled the trend observed in bumblebee abundance, with peak inflorescences recorded in August (fig. 3.3c). However, the density of inflorescences recorded per quadrat was relatively low throughout the season (<15 flowers quadrat^{-1} in June & July, <25 flowers quadrat^{-1} in August). There was a significant effect of management type on inflorescence availability in June and in July (tables 3.4, 3.8, 3.9). Crofter was only significant in June and August (table 3.4). Despite the highest mean number of inflorescences per quadrat within each section occurring in August, variation between management types was greatly reduced when compared to the previous months (figs 3.3a-c, table 3.10). Consequently, the effect of management type on the availability of forage plants was not significant in August (table 3.4). Again, a relatively large proportion of the variation observed within the dataset was explained by the models (R^2 for June: 61%, July: 55%, August: 60%) and this relationship was broadly similar to that observed in July.

3.4.4 The relationship between bumblebee abundance and forage plant availability

The relationship between the numbers of bumblebees and flowers varied throughout the survey period in line with the temporal availability of foraging resources. The Outer Hebrides experienced a prolonged period of unusually dry weather in May 2008, with the islands receiving a total of 12.8 mm of rain compared with an average monthly rainfall in May of more than 50mm (Met Office 2011). Consequently, June was a particularly poor month for flowering plants across the study area and the number of bumblebees per croft section did not vary significantly with flower abundance (χ^2 =

0.27, d.f. = 1 , p = 0.602). Floral abundance increased in July and August across the study area and inflorescence availability became a significant predictor of bumblebee abundance in both months (χ^2 = 8.30, d.f = 1, p = 0.004 in July, χ^2 = 10.67, d.f. = 1, p = 0.001 in August). The amount of variation in bumblebee abundance explained by these models was low (all R^2 values were < 0.1), indicating that models using management type are a better predictor of bumblebee abundance across the study area.

Table 3.8: The effect of management type on floral abundance in June. The t and p values are derived from pair-wise comparisons made between each of the management types, where the relationship is significant the values have been highlighted in bold. Negative t values show that the management types listed along the rows of the table are worse for bumblebees than the management listed as the column heading, and vice versa (**p* = 0.05, ** *p* = 0.01, *** *p* = <0.001).

Management Types	**Arable**		**B & B Mix [a]**		**Fallow**		**Silage**		**Sheep Grazed**		**Mixed Grazing**		**Unmanaged Pasture**	
	t	p	t	p	t	p	t	p	t	p	t	p	t	p
B & B Mix [a]	-0.933	0.35												
Fallow	-0.555	0.58	0.135	0.89										
Silage	**2.124**	*****	**2.557**	*****	1.699	0.09								
Sheep Grazed	0.023	0.98	1.128	0.26	0.593	0.56	**-3.316**	******						
Mixed Grazing	-0.252	0.80	0.563	0.58	0.323	0.75	-1.958	0.05	-0.306	0.76				
Unmanaged Pasture	-1.031	0.31	-0.453	0.65	-0.492	0.62	-1.929	0.06	-1.112	0.27	-0.816	0.42		
Winter Pasture	1.213	0.23	1.92	0.06	1.261	0.21	-0.803	0.42	1.827	0.07	1.207	0.23	1.617	0.11

[a] B & B Mix refers to the Bird and Bumblebee Conservation Mix

Table 3.9: The effect of management type on floral abundance in July. The t and p values are derived from pair-wise comparisons made between each of the management types, where the relationship is significant the values have been highlighted in bold (*p = 0.05, ** p = 0.01, *** p = <0.001).

Management Types	**Arable**		**B & B Mix** [a]		**Fallow**		**Silage**		**Sheep Grazed**		**Mixed Grazing**		**Unmanaged Pasture**	
	t	p	t	p	t	p	t	p	t	p	t	p	t	p
B & B Mix [a]	1.364	0.18												
Fallow	1.373	0.18	-0.074	0.94										
Silage	1.554	0.13	0.474	0.64	0.713	0.48								
Sheep Grazed	1.341	0.19	-0.254	0.80	-0.177	0.86	-1.213	0.23						
Mixed Grazing	1.641	0.11	0.768	0.45	1.068	0.29	0.514	0.61	1.862	0.07				
Unmanaged Pasture	0.601	0.55	-1.116	0.27	-1.057	0.29	-1.368	0.18	-1.065	0.29	-1.518	0.13		
Winter Pasture	1.634	0.12	0.758	0.45	1.048	0.30	0.450	0.65	1.977	0.05	-0.056	0.96	1.513	0.14

[a] B & B Mix refers to the Bird and Bumblebee Conservation Mix

Table 3.10: The effect of management type on floral abundance in August. The t and p values are derived from pair-wise comparisons made between each of the management types, where the relationship is significant the values have been highlighted in bold (**p* = 0.05, ** *p* = 0.01, *** *p* = <0.001).

Management Types	**Arable**		**B & B Mix [a]**		**Fallow**		**Silage**		**Sheep Grazed**		**Mixed Grazing**		**Unmanaged Pasture**	
	t	p	t	p	t	p	t	p	t	p	t	p	t	p
B & B Mix [a]	1.269	0.21												
Fallow	1.787	0.08	0.084	0.93										
Silage	0.401	0.69	-1.017	0.69	-1.009	0.32								
Sheep Grazed	0.638	0.53	-1.062	0.53	-1.376	0.17	0.111	0.91						
Mixed Grazing	0.464	0.64	-0.970	0.64	-1.233	0.22	0.005	0.10	-0.152	0.88				
Unmanaged Pasture	0.443	0.66	-0.442	0.66	-0.471	0.64	0.175	0.86	0.130	0.90	0.179	0.86		
Winter Pasture	0.704	0.48	-0.807	0.48	-1.062	0.29	0.224	0.82	0.227	0.82	0.365	0.72	-0.050	0.96

[a] B & B Mix refers to the Bird and Bumblebee Conservation Mix

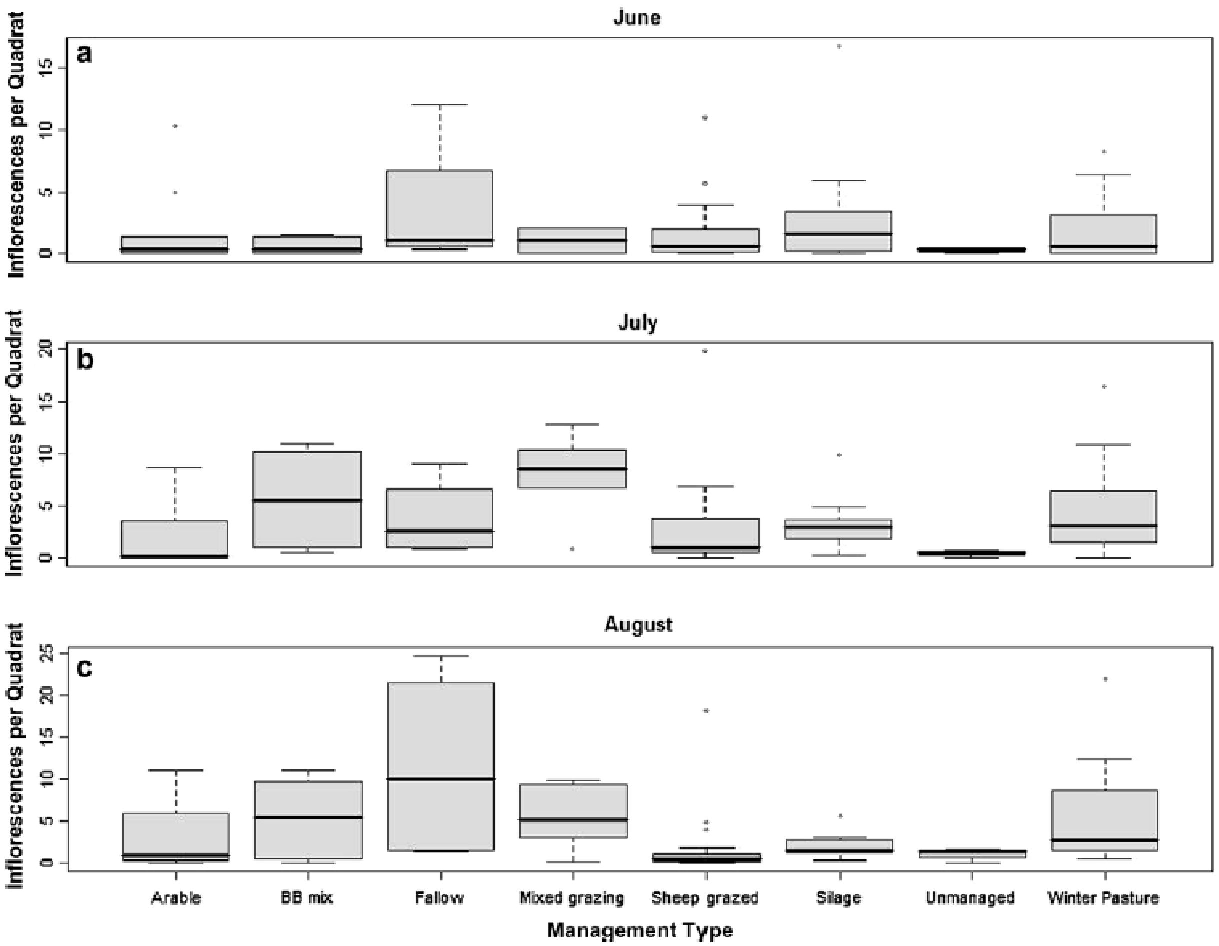

Figure 3.3a-c: Box plots showing variation in the abundance of forage plant abundance across eight different croft management types in June, July and August respectively. Abundance was measured as the mean number of inflorescences recorded per quadrat for each management type. Boxes represent the location of the middle 50 percent of the data and the whiskers indicate the inter-quartile range of the data.

3.4.5 Bumblebee forage plants

The floral resources utilised by foraging bumblebees varied throughout the season (table 3.2). In line with increasing floral abundance and diversity, the number of species visited by bumblebees more than doubled between the beginning of the survey period and August, when a total of 21 flowering plants were utilised. However, it must be noted that many more bees were observed in August, and with more records we would expect to detect more visits to minor food sources.

Early in the season white clover (*Trifolium repens*) and yellow rattle (*Rhinanthus minor*) were the most frequently visited flower species receiving 49% and 30% of all visits in June, respectively. Sections managed as silage and winter pasture contained a high proportion of these two species (between 12% and 65%), and the greatest proportion of yellow rattle (65%) was found in areas of silage. Sheep grazed sections supported the greatest proportion of white clover in flower during June, with over 56% of all inflorescences recorded on this management type. However, no significant relationship was observed between bumblebee and flower abundance in this month.

Visits to white clover declined in July to 33% although it still remained the most frequently visited species and its abundance remained greatest on sheep grazed sections where 63% of this species was recorded. The use of other species increased during July, particularly those belonging to the Fabaceae. Red clover (*Trifolium pratense*) and tufted vetch (*Vicia cracca*) increased from less than 2% of visits each in June to both receiving 13% of visits in July. In contrast to white clover, records of red clover and tufted vetch on sheep grazed sections were negligible with <1% of flowers observed on this land management type. The greatest proportion of red clover was found on fallow and winter grazed areas (38% and 31% respectively), and 19% were recorded on sections sown with the ‘bird and bee’ conservation seed mix. Tufted vetch was less well distributed with over 95% of all inflorescences recorded on the ‘bird and bumblebee’ mix sections. The remaining 5% of flowers were found on silage and winter grazed sections. Overall, 67% of foraging visits observed in July were to species belonging to the Fabaceae.

Fabaceae continued to be the most important forage plant family in August although the proportion of visits declined to 36% in total. The Asteraceae also received a large proportion of total visits (26%) and the Scrophulariaceae were the third most frequently visited family, receiving 11% of foraging visits. All remaining plant families accounted for less than 10% of visits in August.

In August the number of plant species visited by foraging bumblebees was greater than in June and July. However, just three species (red clover, tufted vetch and common knapweed (*Centaurea nigra*) accounted for over 40% of all bumblebee foraging visits in August (table 3.2). Both red clover and common knapweed were predominately found on fallow sections which contained over 75% of all inflorescences recorded belonging to each species during August. The majority (78%) of tufted vetch was recorded on sections of ‘bird and bee’ conservation seed mix, although this species is not included in the ‘bird and bee’ seed mix and must therefore have come from the existing seed bank or seed rain.

3.5 Discussion

The highly intensive nature of farming in Western Europe is considered to be the primary factor driving bumblebee declines (Goulson *et al*. 2008a). However, this study found that even in the relatively low intensity crofting systems in northwest Scotland, bumblebees were present only at very low densities. The limited number of *B. distinguendus* observed on crofts is of particular concern as the study area encompasses some of the few remaining strongholds for this species in the UK (Goulson 2003a; Benton 2006). Although not described as a habitat specialist, *B. distinguendus* is now strongly associated with rare flower-rich machair habitats which are limited in their distribution to Scotland's northwest coast (Angus 2001; Benton 2006). Due to the location of crofts in relation to the machair, only a small proportion of the crofts included in this study encompassed actively managed areas of machair and this could go some way in explaining the limited number of observations of *B. distinguendus* on crofts.

Heterogeneous landscapes are often associated with high species richness (e.g. Weibull *et al*. 2003). Small scale, low intensity agricultural systems promote a mosaic of habitat types and therefore they are often considered to be of benefit to biodiversity compared with more intensive systems. However, studies of bumblebee diversity in low intensity agricultural systems in Estonia have demonstrated that even in these heterogeneous farming systems, the adjacent non-agricultural habitats supported a greater diversity of bumblebee species (Mänd *et al.* 2002). Although we did not include habitats adjacent to crofts in this study, these non-agricultural areas could potentially be providing important foraging resources for bumblebees and therefore explain why such low numbers were recorded on crofts. During the period of fieldwork we observed more than 20 *B. distinguendus* on roadside verges but only 2 on the crofts in our study (N. Redpath & L. Osgathorpe pers. obs.). Research into this area is on-going. Non-croft habitats may also provide hibernation and nesting sites, two key ecological requirements which are important factors for bumblebee conservation, and we recommend that further research in this area is conducted.

3.5.1 *The effect of land management type on the abundance of bumblebees and their forage plants*

In general, the 'bird and bee' conservation mix, fallow and silage were the land management types which supported the greatest number of bumblebees. However, the efficacy of each of these management types in attracting foraging bumblebees varied throughout the season which reiterates the importance of a heterogeneous agricultural landscape (Weibull *et al*. 2003). Significantly more foraging bumblebees were observed on areas of crofts which were not sheep grazed. The absence of livestock in the summer allows plants to flower and set seed, whilst grazing in the winter promotes plant species diversity by creating an open sward which allows wildflowers to compete with grasses (Stewart & Pullin 2008). In particular, our findings demonstrate that there is a marked negative relationship between the abundance of foraging bumblebees and sheep grazing. Even at low density, sheep grazed pasture supported negligible numbers of bumblebees and therefore management of sheep is a key factor in determining the value of crofts for bumblebees. Previous studies have revealed a benefit of cattle grazing over sheep grazing or unmanaged pasture in maintaining bumblebee diversity and abundance (Carvell 2002), but we were unable to survey pasture grazed solely by cattle as any cattle present were in a mixed livestock system.

In August, sections of ‘bird and bee’ conservation mix and silage supported significantly more bumblebees than other management types. Although these sections supported a lower abundance of bumblebee forage material than fallow or winter grazed sections they contained the highest proportions of red clover and tufted vetch which were two of the most frequented species by foraging bumblebees during August. However, it should be noted that tufted vetch was not a component of the sown mix and therefore its presence in these sections must be a result of the existing seed bank or seed rain from the surrounding area. This suggests that it is the availability and abundance of certain key plants and not the overall diversity of forage material which is important for maintaining bumblebee populations throughout the season. This is exemplified by our results which show that although the range of forage plants available was greatest in August, foraging bumblebees predominantly visited only three species.

3.5.2 Management recommendations for bumblebee conservation

The data presented here demonstrate that crofting practices in northwest Scotland are not currently supporting high numbers of bumblebees or their forage plants. Whilst some land management types have been identified as more beneficial than others in promoting forage plant availability and bumblebee abundance, the low overall number of bumblebees recorded on crofts would suggest that none of the management types surveyed are of great benefit to the conservation of bumblebees.

Sheep grazing on crofts is on the increase partly due to the dramatic increase in sheep numbers in these areas since the 1940s (Hance 1952; Willis 1991). Stocking densities, particularly sheep densities, are increasing habitat homogeneity across crofted areas as sheep grazing has a particularly detrimental effect on floral diversity and abundance. In turn, this has a negative impact on the number and diversity of bumblebees which are able to exploit the remaining limited forage resources. If populations of rare bumblebees are to persist in crofted regions, we would strongly recommend a return to the historically traditional grazing regimes which ensure livestock are grazed on lowland areas in the winter and put out to graze on the hill and moor lands in the summer months, allowing the lowland grassland areas to flourish and flower. If this is not always practical, then an alternative possibility may be to increase sheep density in some areas, thereby allowing others to be left ungrazed on a rotational basis.

The species composition and abundance of foraging resources are important for maintaining the diversity of foraging bumblebees (Goulson *et al*. 2008b). This study supports previous work which suggests that sufficient areas of key forage plants are of importance when conserving bumblebees, even within low intensity agricultural systems (Mänd *et al*. 2002). The provision of forage material throughout the entire bumblebee season, from the time when queens emerge from hibernation throughout the summer until the reproductives are produced is particularly important (Bäckman & Tiainen 2002; Westphal *et al*. 2006). Successional sowings of conservation seed mixes may achieve this lengthy flowering period (Carreck & Williams 2002), and the inclusion of spring flowering species would also be of additional conservation value to nest founding queen bumblebees (Lye *et al*. 2009).

Several studies have helped to identify which conservation seed mixes are most useful for foraging bumblebees (e.g. Carvell *et al*. 2007). However, to date, research has been focussed almost exclusively on intensive lowland farms in England (Pywell *et al*. 2004; Pywell *et al*. 2006; Carvell *et al*. 2007). In areas of low intensity agriculture such as the crofted regions of Scotland the implementation of bumblebee conservation measures is perhaps more pressing than previously thought. Conservation measures for bumblebees on crofts should perhaps not aim to maximise floral diversity but instead increase the availability of a narrower range of key plant species. It is possible that a greater diversity in the plant community may support a greater diversity of invertebrates, but for bumblebees, a number of key forage plant species appears to be more important than the creation of diverse swards. In addition, *Protapion ryei*, an endemic species of weevil and also a UK BAP species, is found only in the Northern and Western Isles of Scotland and relies on red clover as a larval food source. Therefore, promoting clover rich seed mixes for the conservation of bumblebees may also be of benefit to this rare weevil. However, we also recognise that a broad range of flowering species may be of greater benefit to a larger suite of invertebrates not considered in this study.

The results of this study show that despite the use of a wide range of flower species by foraging bumblebees throughout the summer, over 44% of all visits were to just three species belonging to the Fabaceae (red clover, white clover and tufted vetch). This supports work by Goulson and Darvill (2004) showing that 65% of bumblebee foraging visits on Salisbury plain were to just six species.

3.5.3 Conclusions

Although current croft management techniques do not support significant numbers of bumblebees, crofting can still play an important role in their conservation. This could be achieved through the adoption of agri-environment schemes tailored specifically for low-intensity systems but these are not currently available. In order to encourage bumblebees, particularly the rare long-tongued species such as *B. distinguendus*, to thrive within the crofted regions of northwest Scotland we recommend the development of targeted schemes which promote the implementation of bumblebee-specific seed mixes in conjunction with the late cutting of grass crops. Mixes containing a high proportion of Fabaceae, specifically red and white clover, have been identified as important for bumblebees within agricultural landscapes elsewhere in Europe (Bäckman & Tiainen 2002; Goulson & Darvill 2004; Goulson *et al*. 2005; Carvell *et al*. 2006; Diekötter *et al*. 2006). Our research suggests that these Fabaceae-rich mixes would also be highly appropriate within the context of bumblebee conservation in northwest Scotland. We also recommend that payments for the removal of sheep from lowland areas during the summer months should be included in future agri-environment schemes. This would help to ensure that the floral diversity added to the landscape through the use of conservation seed mixes is not compromised and also potentially enable natural regeneration of sward diversity in otherwise overgrazed areas.

4 The great yellow bumblebee (*Bombus distinguendus)* and the corncrake (*Crex crex*) – A combined species approach to habitat management in the Outer Hebrides

4.1 Abstract

The Great Yellow Bumblebee, *Bombus distinguendus*, is outlined as a priority species for conservation by the UK Biodiversity Action Plan (UKBAP). Once widespread throughout the UK, *B.distinguendus* is now restricted to the North and West of Scotland, becoming particularly associated with species-rich machair grassland. Within the current geographical range of *B. distinguendus*, considerable effort is being made to conserve another UK Biodiversity Action Plan species, the Corncrake (*Crex crex).* This species has suffered a significant decline over the last 100 years as a result of changes in agricultural practice, particularly changes in grassland management. In addition to implementing appropriate grassland management, farmers and crofters are encouraged to create areas of tall vegetation in which corncrakes can nest early on in the season. These early cover areas are then able to provide a refuge for corncrakes both early and late in the season once hay and silage crops have been harvested and there is little cover available in the wider agricultural landscape. In an attempt to enhance the conservation benefit of existing land management agreements, the RSPB has improved the suitability of a number of early cover sites for foraging bumblebees. This study focused on assessing a total of 21 early cover plots (ECPs) situated within five principle areas of the Outer Hebridean Island of North Uist. The number of foraging bumblebees observed in ECPs managed for corncrakes was consistently low throughout the survey period. This research has shown that current management in ECPs for *C. crex* are

largely ineffective in terms of providing foraging resources for *Bombus* species and therefore, in areas where *B. distinguendus* continues to thrive, conservation efforts should be concentrated on the maintenance and restoration of species-rich grassland habitats such as machair.

4.2 Introduction

Agricultural intensification and the subsequent loss of semi-natural habitats have been identified as the probable cause for a widespread loss of biodiversity across much of Western Europe (Chamberlain *et al*. 2000; Robinson & Sutherland 2002). More specifically, these factors are responsible for a marked decline in bumblebee populations in recent decades (Goulson 2003; Benton 2006; Goulson *et al*. 2008). A considerable body of research has documented the decline of bumblebees but the most appropriate methods for managing suitable habitat in order to halt this decline requires further research.

The Great Yellow Bumblebee, *Bombus distinguendus*, is outlined as a priority species for conservation by the UK Biodiversity Action Plan (UKBAP). Once widespread throughout the UK, *B.distinguendus* is now restricted to the north and west of Scotland and the species has become particularly associated with species-rich machair grassland (Benton 2006). However, the historic geographical range of *B. distinguendus* includes regions of the UK where machair does not occur and thus the species is not considered to be a habitat specialist (Goulson *et al*. 2006). Machair is a habitat of great importance to a number of rare and declining species and is a priority habitat for conservation as outlined by the UK Biodiversity Action Plan and the European Habitats Directive (Love 2003; JNCC 2010).

4.2.1 Grassland management and corncrake conservation

The Royal Society for the Protection of Birds (RSPB) and the *Bombus* Working Group (BWG) were designated the lead partners for *B. distinguendus* when it became a UK Biodiversity Action Plan priority species in 1999. The UKBAP outlines the need to maintain populations found on Sites of Special Scientific Interest and on RSPB reserves, with the long term objective of enhancing the existing population size by 2010.

Within the current geographical range of *B. distinguendus*, considerable effort is being made to conserve another UK Biodiversity Action Plan species, the Corncrake, *Crex crex.* This elusive farmland bird has suffered a significant decline and range contraction over the last 100 years as a result of changes in agricultural practice and in particular, changes in grassland management (Stowe *et al*. 1993; Green 1995; Green *et al*. 1997; Tyler *et al*. 1998). Very few birds remain in England and Wales and, similarly to *B. distinguendus*, this species now exists predominantly in the Hebridean islands and parts of Orkney.

Corncrakes migrate to Africa in the autumn and return to Europe in the spring to breed. The first brood of chicks is reared in tall, spring vegetation or ‘early cover’ and then later in the year, once grassland adjacent to the early cover vegetation has grown tall enough to conceal the birds, female corncrakes often move into the grassland areas and produce a second brood (Niemann 1995; Green *et al*. 1997; Tyler 2006). The management of grassland habitats has been identified as the main factor influencing the breeding success of corncrakes, and the aspect of grassland management which has been recognised as having the most significant impact on *C. crex* breeding success is the timing and direction of mowing (Stowe *et al*. 1993; Green 1995; Sime *et al*. 1996). Female corncrakes and their chicks often become trapped in a central fragment of grassland as mowers move from the field periphery into the field centre. Reluctant to move through the exposed environment of newly cut stubble in order to escape, corncrakes are often killed by mowers and it is estimated that more than 50% of chicks are killed in this way (Tyler *et al.* 1998). In addition to this, the development of fast growing grass species and the use of artificial fertilizers enable grass crops to be harvested earlier in the year, when corncrake chicks are still immature and unable to fly and are therefore less able to escape mowers (Green 1995).

One method which has improved this situation has been the implementation of corncrake-friendly mowing techniques. This process involves mowing from the centre of the field, in an outwards direction, driving corncrakes out into the safety of hedgerows and field margins (Sime *et al*. 1991; Tyler 1996; Tyler *et al.* 1998). In addition to these mowing specifications, agreements have been created with landowners in areas known to support corncrakes. These land management agreements stipulate the late cutting of silage and hay crops in conjunction with corncrake-friendly mowing techniques and by doing so they allow chicks, particularly from the second brood, a greater chance of survival (Green 1995).

In fields which support native wildflowers such as red clover (*Trifolium pratense*), common knapweed (*Centaurea nigra*) and tufted vetch (*Vicia cracca*), the benefits of late mowing are also applicable to bumblebees. Bumblebees require continuous access to suitable forage material throughout the summer season as, unlike honey bees; they only store pollen and nectar for a few days at a time (Bäckman & Tiainen 2002;

Westphal *et al*. 2006). The production of silage instead of hay allows grass crops to be cut earlier in summer, which in turn removes large potential bumblebee forage patches. For this reason, delayed cutting may be of benefit to a number of *Bombus* species. However, it is important to recognise that the widespread move towards more intensified farming techniques has included the 'improvement' of grassland habitats with the application of artificial fertilizers. The increased nutrient status of improved grasslands often renders them unsuitable for the persistence of many native wildflower species (Walker *et al*. 2004). Fertilisers enhance the growth of fast growing grass species, which subsequently out-compete wildflower species that have evolved to grow in nutrient poor soils and therefore, late cutting of grass crops alone may not provide sufficient foraging resources.

In addition to implementing appropriate grassland management, farmers and crofters are encouraged to create areas of tall vegetation in which corncrakes can nest early on in the season, when adjacent grassland habitats are not yet tall enough to conceal the birds (Green 1995; Green 1997). This 'early cover' typically consists of nettles (*Urtica dioica*), iris (*Iris pseudacorus*) or cow parsley (*Anthriscus sylvestris*), all of which establish early in the year and conceal corncrakes whilst they produce their first brood (Stowe *et al*. 1993; Green *et al*. 1997). Both government agencies and non-government organisations such as the RSPB have undertaken a number of management agreements with landowners to prevent these areas of early cover from being cut or grazed during the summer. These early cover areas are then able to provide a refuge for corncrakes both early and late in the season once hay and silage crops have been harvested and there is little cover available in the wider agricultural landscape (Green 1995).

4.2.2 Corncrake and Great Yellow bumblebee habitat management

Bombus distinguendus forages on a range of common native wildflower species (see chapter 2) and the successional availability of such species, from mid May through until mid September, is of great importance (Charman 2007). However, by September much of the agriculturally managed grassland in the UK has been harvested for either hay or silage, even in areas that encourage delayed mowing as part of corncrake habitat agreements. The early harvesting of grass crops potentially removes large areas of foraging resources at a critical period in the bumblebee colony cycle, when reproductives are being produced. Therefore, areas of land that are protected from cutting and grazing until the end of the summer could potentially provide islands of foraging resources for later emerging bumblebee species such as *B. distinguendus*.

Due to the similar distribution of the species, land management agreements, which stipulate the creation and maintenance of corncrake early cover habitat have been established across much of *B. distinguendus'* current range. In an attempt to enhance the conservation benefit of these existing land management agreements, the RSPB has improved the suitability of a number of early cover sites for foraging bumblebees. This has been achieved by either sowing conservation seed mixes or by creating fallow areas, both of which are combined with restricted mowing and grazing throughout the summer in order to benefit corncrakes. This study assesses the success of this combined species approach to habitat management by quantifying the abundance of foraging bumblebees in early cover areas and establishes which land management practices are the most effective at enhancing early cover for bumblebees.

4.3 Methods

4.3.1 Study sites

Areas of early cover, which are managed either directly by RSPB staff or indirectly via management agreements with land owners, shall be referred to from here on as early cover plots (ECPs). A total of 21 ECPs were randomly selected for surveying from a possible 47 ECPs. All ECPs were situated within five principle areas (Balranald, Hosta, Clachan, Solas and Paibeil; fig. 4.1) of the Outer Hebridean Island of North Uist, known to support key populations of both *B. distinguendus* and *C. crex*. The ECPs ranged in area from approximately 296 m^2 to 4267 m^2.

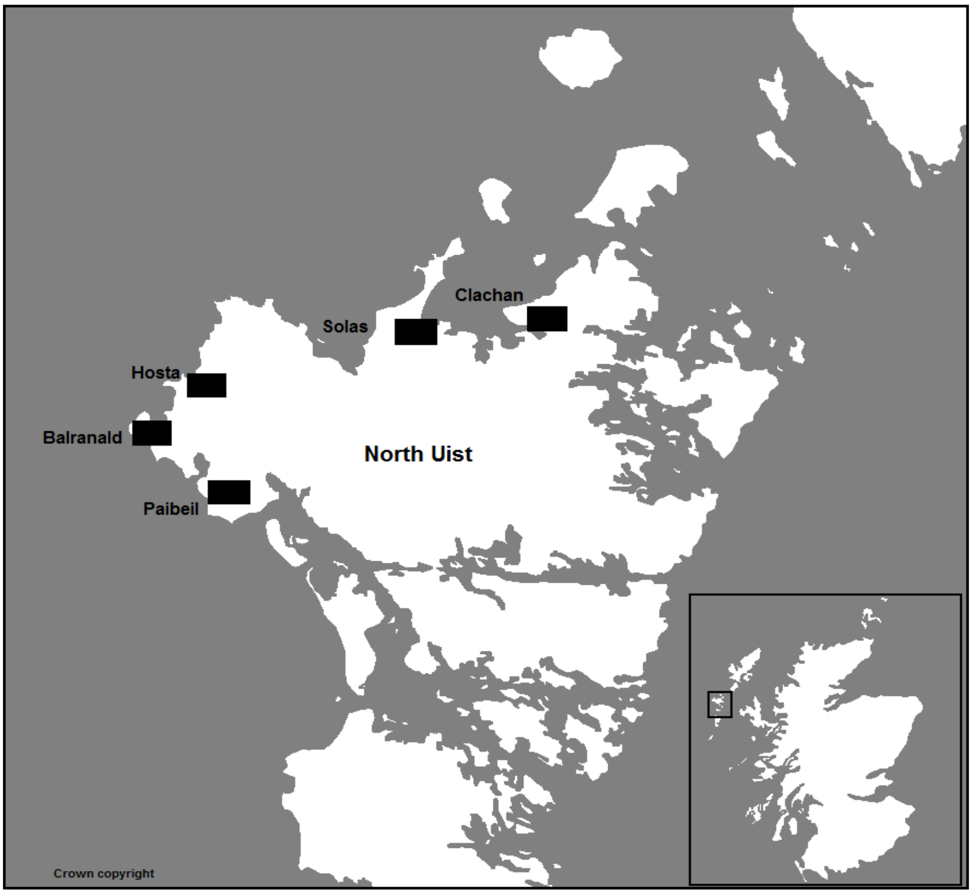

Figure 4.1: The location of the principle areas of machair and corncrake early cover surveyed, Isle of North Uist, Scotland

Three principle land management practices had been implemented within the ECPs and these were; ploughing and leaving fallow (PF) (two plots), ploughing and sowing a 'wild bird cover' (WBC) seed mix enhanced with *Phacelia tanacetifolia* and *Trifolium pratense* (five plots), and plots in which no active management (NM) was implemented other than restricted mowing and/or grazing between 31st March and 1st September (14 plots). The mowing/grazing restriction was applicable to all three ECP management types. In addition, four areas of machair were surveyed as this habitat is known to provide important forage material for *B. distinguendus* in the Outer Hebrides (Goulson 2003a; Benton 2006). Therefore, these sites could be compared with the ECP management types in order to establish their efficacy in providing bumblebee forage material. The four areas of machair were located within similar geographical areas of North Uist as the ECPs (Balranald, Clachan, Solas and Hosta but not Paibeil as there was no accessible machair in this area; fig. 4.1).

4.3.2 Bumblebee sampling methods

Each ECP was surveyed for the presence of foraging bumblebees three times between August 9th and 22nd 2007. This time period was selected because as a later emerging bumblebee species, this is when *B. distinguendus* population numbers are likely to be at their highest (Benton 2006).

A transect line was established along a single edge of each ECP. Bumblebees observed foraging within 2 meters of the transect line, on the ECP side only, were recorded. To avoid, as far as possible, the multiple recording of individual bees, the transect line was walked at a constant speed and the vegetation was visually scanned for bumblebees at a 45º angle to the transect path. This 'bee walk' methodology was adapted from the standard butterfly recording protocol developed by Pollard (1977). In order to avoid disturbing nesting corncrakes, it was not possible to walk centrally positioned transects through each ECP. A transect line was established at each of the four machair sites and foraging bumblebees were recorded as before and along one side of the transect line only in order to allow comparison with the ECP data.

Surveys took place between 08:00 and 18:00 hours, in dry weather and when temperatures exceeded 12 °C. Bumblebees were identified to species level but the caste was not recorded. The plant species on which bumblebees were observed foraging was also recorded.

4.3.3 Vegetation sampling methodology

Since it was not possible to enter ECPs for vegetation surveys, a visual estimate of the percentage cover of each plant species known to be utilized by foraging bumblebee was recorded for the whole plot. Vegetation surveys were not undertaken on the areas of machair but the plant species on which bumblebees were observed foraging were recorded.

4.3.4 Data analysis

The effect of ECP management type on abundance of foraging bumblebees was examined using generalised linear models (GLM) with Poisson errors in the software package R version 2.10.1. ECP management type (PF, WBC, NM) was included in the model as a factor and the percentage cover of forage plant species was included as a covariate. Pair-wise post hoc comparisons were conducted to assess differences in bumblebee abundances between management types. Transect length was used as an offset in the model to account for the differences in the total areas of each management surveyed. The efficacy of ECPs in attracting foraging bumblebees was assessed by comparing bumblebee abundance on ECPs with bumblebee abundance on floristically-rich machair habitat using Mann-Whitney U tests.

4.4 Results

4.4.1 Bumblebee species and habitat type

Throughout the survey period, a total of 3606m and 646m of transect were walked in ECPs and on machair grassland respectively. A total of 360 foraging bumblebees were observed; all five *Bombus* species native to the study area were recorded during the survey period, including two UKBAP species, *B. distinguendus* and *Bombus muscorum* (table 4.1).

Table 4.1: The proportion of each *Bombus* species observed foraging on both *C. crex* early cover plots (ECPs) (*n* =245) and machair habitats (*n* = 115).

Species	% Total bumblebees machair	% Total bumblebees ECPs
Bombus distinguendus	22.6	5.7
Bombus muscorum	75.7	69.4
Bombus lucorum	0.0	13.9
Bombus jonellus	0.0	1.6
Bombus hortorum	1.7	9.4

Bombus muscorum was the most commonly observed species in both habitat types with a total of 257 individuals recorded. *Bombus distinguendus* was the second most frequently recorded species on the machair sites but was one of the two least commonly recorded species on ECPs. *Bombus jonellus* was not observed at any of the machair sites and was the least frequently observed species overall.

The abundance of bumblebees observed in the two habitat types differed significantly (w=244, p=0.035). Based on the median number of bees, the abundance of bumblebees per 100 meters was more than seven times greater on machair habitat than in the ECPs. The abundance of *B. distinguendus* was significantly higher on machair habitat than on ECPs and a similar pattern was observed for *B. muscorum* (w=240, p=0.016) and (w=243, p=0.028) respectively, with this species occurring eight times more frequently on machair than in ECPs. The abundances of *B. lucorum*, *B. hortorum* and *B. jonellus* were relatively low across both habitat types and no significant differences in abundance were found between machair and ECPs (fig. 4.2).

Bombus distinguendus was recorded foraging on seven of the 21 ECPs surveyed. These seven ECPs were distributed across the five principle survey areas and encompassed all three ECP management types. Three of the ECPs were sown with wild bird cover crop (WBC), three were managed solely by restricted grazing/mowing (NM) and the final ECP was ploughed and left fallow (PF). ECP management type was found to significantly affect both overall bumblebee abundance and the abundance of *B. distinguendus* (table 4.2). Pair-wise comparisons revealed that ECPs sown with wild bird cover (WBC) attracted significantly more foraging bumblebees than ECPs that were ploughed and left fallow (PF) (z = 2.367, p = 0.017). ECPs sown with wild bird cover crop seed mix also attracted significantly more foraging bumblebees than ECPs that were not mown/ungrazed (NM) only (z = 2.727, p = 0.006). There was no significant difference observed in the abundance of foraging bumblebees on ECPs that were ploughed and left fallow or not mown/ungrazed only.

4.4.2 Forage plant use

Six plant species were utilized by bumblebees foraging on machair sites and fifteen species were utilized by bumblebees foraging on ECPs (table 4.3). Of the six plant species utilized by bumblebees foraging on machair, *B. distinguendus* was recorded foraging on only three, *C. nigra*, *T. pratense* and *Senecio jacobaea.* Across the ECPs, *B. distinguendus* was observed foraging on five different plant species, *S. jacobaea*, *V. cracca*, *C. nigra*, *Phacelia tanacetifolia* (a non-native species included in the wild bird cover seed mix) and *Cirsium vulgare.*

4.4.3 Forage plant availability

Ten plant species, known to be utilised by foraging bumblebees, were recorded across the four machair sites (Benton 2006; Charman 2007). A total of 20 forage plant species were recorded across the 21 ECPs during the survey period. The estimated total percentage cover of bumblebee forage plant material in each ECP ranged from between 0 and 61%. The estimated total percentage cover of forage plant material in each ECP had a significant effect on bumblebee abundance (table 4.2; fig. 4.3) and more specifically had a significant effect on the abundance of *B. distinguendus* (table 4.2).

Table 4.2: A summary of test statistics derived from the generalised linear model examining the effect of ECP management type and the percentage cover of bumblebee forage plant material on the abundance of bumblebees in 21 ECPs surveyed on the Island of North Uist, Outer Hebrides (**p*=0.05, ***p*=0.01, ****p*=<0.001).

	All bumblebees	***B. distinguendus***
Management	$\chi^2_2 = 223.32$*	$\chi^2_2 = 21.95$*
Percentage cover	$\chi^2_1 = 156.93$***	$\chi^2_1 = 15.51$*

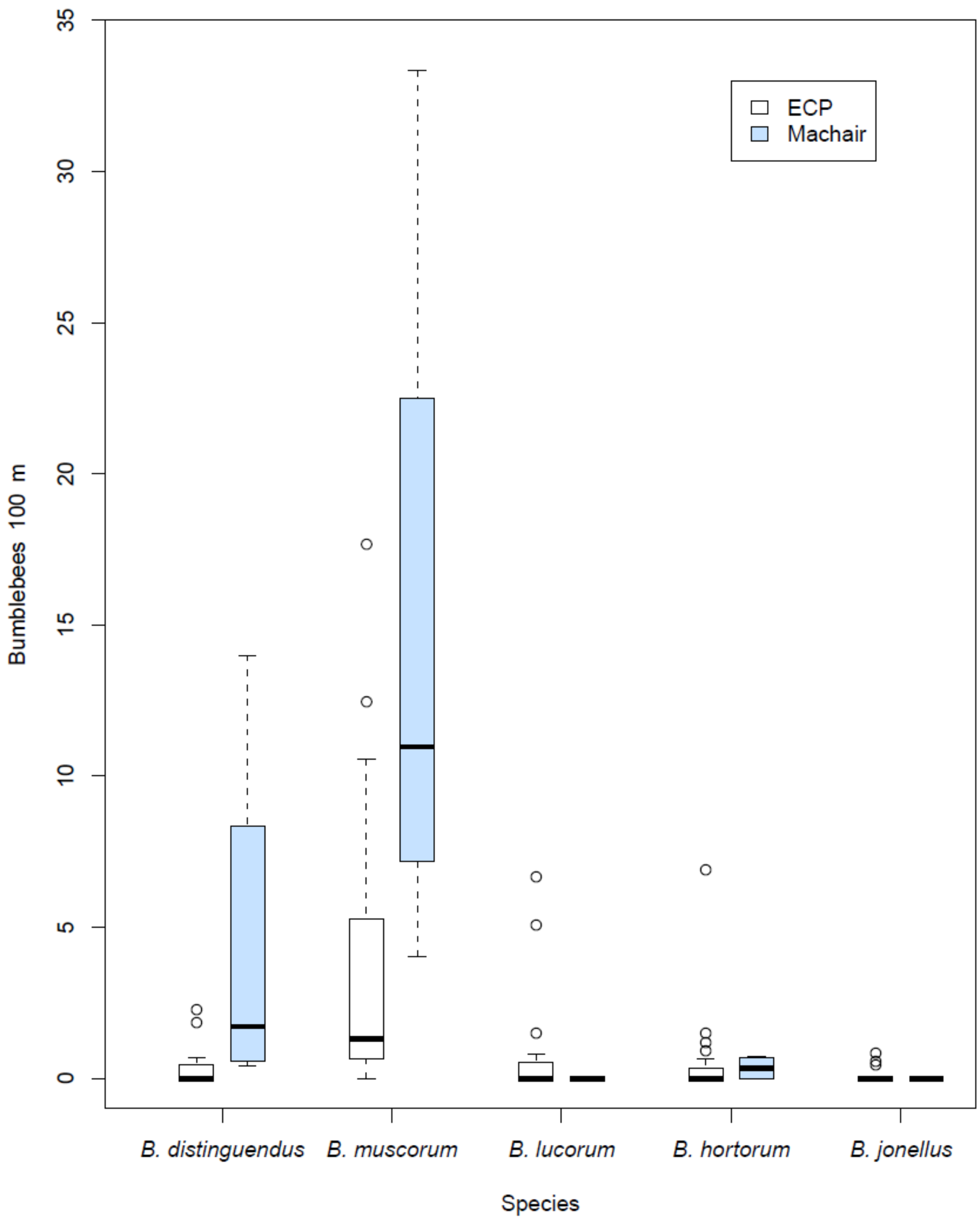

Figure 4.2: The median number of bumblebees observed foraging per 100 meters of transect in two habitat types, early cover plots (ECPs) managed for *Crex crex* and machair grassland. The boxes represent the median and the 25-75% quartile range and the circles indicate outliers.

Table 4.3: The proportion of observed foraging visits to each forage plant species on both machair and early cover plots, with the relative availability of each forage plant species in early cover plots given as a mean % cover (this information was not available for machair sites as the areas were too large to estimate total % cover). The percentages marked with an asterisk denote plant species on which *Bombus distinguendus* was observed foraging.

Forage plant species	**Family**	**Machair % of total bumblebee visits**	**Mean % cover per ECP**	**ECPs % of total bumblebee visits**
Arctium minus	Asteraceae	0.00	0.10	0.41
Centaurea nigra	Asteraceae	74.78*	3.43	38.40*
Cirsium arvense	Asteraceae	0.00	1.67	0.41
Cirsium vulgare	Asteraceae	0.00	1.14	3.27*
Leontodon autumnalis	Asteraceae	3.48	0.33	2.86
Senecio jacobaea	Asteraceae	4.35*	2.81	4.90*
Sonchus arvensis	Asteraceae	0.00	0.52	0.41
Raphanus sativus	Brassicaceae	0.00	2.90	3.67
Succisa pratensis	Dipsacaceae	0.00	0.05	1.22
Lathyrus pratensis	Fabaceae	0.00	0.24	0.41
Lotus corniculatus	Fabaceae	0.00	0.10	0.41
Trifolium pratense	Fabaceae	10.43*	2.38	4.49
Trifolium repens	Fabaceae	6.09	0.10	0.00
Vicia cracca	Fabaceae	0.00	2.48	23.30*
Vicia sepium	Fabaceae	0.00	0.48	8.57
Phacelia tanacetifolia	Hydrophyllaceae	0.00	1.10	6.94*
Odontites verna	Scrophulariaceae	0.87	0.24	0.41

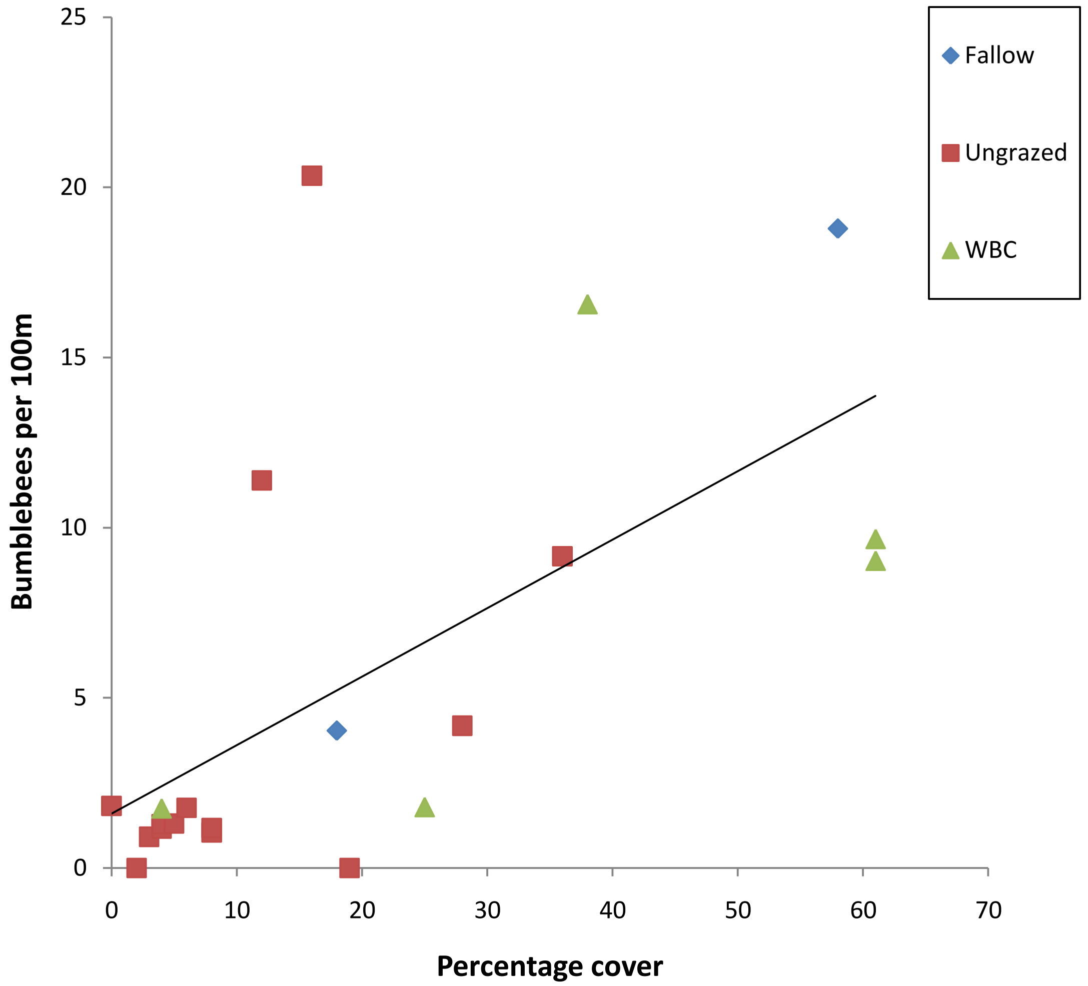

Figure 4.3: The relationship between the percentage cover of forage plant species and the abundance of foraging bumblebees in ECPs under three different management regimes.

4.5 Discussion

The number of foraging bumblebees observed in ECPs managed for corncrakes was consistently low despite the presence of 20 plant species known to provide bumblebee forage being recorded across the 21 ECPs. In particular, *Bombus distinguendus*, one of the two most commonly observed *Bombus* species on machair, was one of the least frequently observed species in ECPs, suggesting that these areas are not being managed in a way that is effectively attracting the rarest UK bumblebee species.

Three of the seven ECPs in which *B.distinguendus* was recorded were sown with the wild bird cover seed mix and this was the ECP management type that was found to attract the most foraging bumblebees. However, only half the *B. distinguendus* foraging visits recorded in ECPs sown with a wild bird cover seed mix were to a specifically sown species (*P. tanacetifolia*). The remaining foraging visits were to species not sown in the original seed mix and so must have arisen from the seed bank or from seed rain. These findings are supported by work carried out across crofted land in northwest Scotland in 2008. Redpath *et al*. (2010) (see chapter 3) found that areas sown with conservation mixes designed to attract both birds and bees did attract foraging bumblebees but that the majority of bumblebee foraging visits within these areas were to species not sown directly. It should also be noted that *P. tanacetifolia* is a non-native species, and hence the validity of sowing this species on or near species-rich machair grasslands is questionable.

Where key plant species are scarce or non-existent, the implementation of seed mixes can help fill the forage gap (Carreck & Williams 2002) and research in England has demonstrated that seed mixes containing legumes attract a high number of bumblebees within an agricultural landscape (Carvell *et al*. 2007). However, the wild bird cover seed mix, sown in five of the 21 ECPs, contained very little Fabaceae, a family known to be important for a number of *Bombus* species, particularly the rarer, long-tongued species which includes *B. distinguendus* (Goulson *et al*. 2005; Goulson *et al*. 2006). This would suggest that whilst the wild bird cover seed mix may provide forage for over wintering passerines, and allow corncrakes to be concealed by spring vegetation, it has not been designed to satisfy the requirements of foraging bumblebees. If this wild bird cover seed mix is to be utilized in the future, to attract foraging bumblebees it will require some significant changes to the species composition i.e. the addition of key bumblebee forage plant species. Bumblebees do not necessarily require a broad range of flowering plant species but they do require the continuous availability of certain key plant species throughout the flight period (Bäckman & Tiainen 2002; Mänd *et al*. 2002; Goulson *et al*. 2008b), and the ECPs appear to be generally lacking in these key species.

Plants which are important for a number of *Bombus* species, including *B. distinguendus,* and which have also performed well in habitat restoration projects include *T. pratense, L. corniculatus* and *C. nigra* (Carvell *et al*. 2006). These three species are native to the study area and two of them (*T. pratense* and *C. nigra*) were the most frequently utilized species by foraging bumblebees across the machair sites surveyed during this study. For these reasons we would recommend their inclusion in seed mixes which are to be used in future bumblebee habitat restoration projects within this geographic region.

A landscape scale approach to bumblebee conservation is also important (Dramstad *et al*. 2003). Ideally, *B. distinguendus* requires large expanses of unimproved flower-rich habitat (Edwards 1997). Therefore, not only do seed mixes which contain a high proportion of *B. distinguendus* forage plant species need to be produced, but they also need to be distributed across the current geographical range of the species in order to support populations effectively. Sowing specific seed mixes in conjunction with restricted summer grazing, particularly of sheep which preferentially graze flower heads and therefore prevent wildflowers from setting seed, is important when managing habitat for rare and declining bumblebees (Redpath *et al*. 2010). However, some disturbance of grassland can positively influence bumblebee forage plant availability when compared with completely unmanaged grassland. Areas of Salisbury plain which were not cattle-grazed for a two year period showed decreased bumblebee abundance and a reduced availability of their forage plants when compared with areas which had experienced some degree of disturbance (Carvell 2002). The results presented here suggest that winter grazing alone is not a sufficient management strategy for improving bumblebee forage plant availability. The ECPs that were winter grazed only supported very few foraging bumblebees, indicating that suitable grazing regimes should be implemented in conjunction with appropriate seed mixes if forage plant species are to proliferate.

4.6 Conclusion

This study shows that whilst parallels may be drawn between the decline of the *C. crex* and *B.distinguendus*, habitat management for *C. crex* does not necessarily benefit *B. distinguendus.* Current management in ECPs for *C. crex* appear largely ineffective in terms of providing foraging resources for *Bombus* species. In areas where *B. distinguendus* continues to thrive, conservation efforts should be concentrated on the maintenance and restoration of species-rich grassland habitats such as machair. Machair is an important resource for foraging bumblebees in the Outer Hebrides and agri-environment schemes which promote and restore semi-natural grassland will benefit not only the focal species such as *B. distinguendus,* but by enhancing these areas for foraging bumblebees they are also likely to improve the pollination of crops and native wildflowers in the wider landscape (Öckinger & Smith 2007).

5 Is the existing seed bank sufficient for restoring bumblebee foraging resources on areas of degraded machair grassland?

5.1 Abstract

Machair is a type of species-rich coastal grassland found only in the northwest of Scotland and western Ireland. It supports significant populations of a number of rare and declining species including the great yellow bumblebee (*Bombus distinguendus*), which has suffered widespread declines in recent decades and is now strongly associated with florally rich machair habitats. However, the floral diversity of machair is increasingly under threat due to changes in land management practices. Traditionally, small scale, low intensity cropping and rotational grazing have promoted species diversity but increased grazing pressure and reduced cropping have resulted in substantial areas of degraded machair, which exhibits low floral diversity. Finding methods with which to restore floral diversity to these areas, in order to maintain suitable foraging habitat for rare bumblebees, has become a conservation priority. One option to be considered when investigating strategies for restoring grassland habitats such as machair is manipulation of the existing soil seed bank. This research quantifies the abundance of dicotyledonous species found in the seed bank at nine machair sites in the Outer Hebrides, Scotland, and compares this with the species present in the existing vegetation. The seedling emergence technique was used to establish which species were present in machair soils. A total of 23 dicotyledonous species were recorded in the seed bank and this research indicates that the machair seed bank at these sites has a seed density comparable with that of other calcareous grasslands. However, the absence of certain key machair species in the seed bank indicates that the addition of seed may be

necessary in order to ensure the restoration of wildflower-rich machair habitats for the conservation of foraging bumblebees.

5.2 Introduction

Across Europe, species-rich grassland habitats have become increasingly degraded as a result of intensified agricultural practices (Muller *et al*. 1998). Machair is a coastal grassland habitat unique to northwest Scotland and western Ireland, with the largest and arguably the best examples of machair situated in the Outer Hebrides (Angus 2001; Hansom & Angus 2005). Not only is this habitat important from a botanical perspective, but it also supports populations of several nationally and internationally rare bird species. These include corn bunting (*Emberiza calandra*), twite (*Carduelis flavirostris*), corncrake (*Crex crex*), lapwing (*Vanellus vanellus*), redshank (*Tringa totanus*), dunlin (*Calidris alpina*) and ringed plover (*Charadrius hiaticula*) (Wilson 1978; Jackson & Green 2000; Wilson *et al.* 2007; Beaumont & Housden 2009; Wilkinson & Wilson 2010). Machair has also become an important habitat for invertebrate species, including the threatened great yellow bumblebee, *Bombus distinguendus*, which has declined significantly in recent decades and is now heavily reliant on this floristically diverse grassland habitat (Benton 2006; Goulson *et al*. 2006).

Recent increases in grazing pressure, a reduction in traditional cropping practices and in some areas, a complete lack of grazing and management, has resulted in areas of degraded machair that exhibit low floral diversity (JNCC 2010). Traditionally, crofting practices divided machair grassland into strips of arable and fallow land of varying age and maturity (Roberts *et al*. 1959). Combined with the winter grazing of cattle and sheep, these agricultural practices are considered to be fundamental in the creation of florally diverse, species-rich machair (Owen *et al*. 2001; Kent *et al*. 2003). Although intensive agriculture has not affected the most north-westerly fringes of Scotland to the same extent as it has much of Western Europe, the current trend for over grazing and increased silage production has undoubtedly resulted in changes to machair sward composition (UK Biodiversity Action Plan 2007; 'JNCC' 2010). Conversely, the complete abandonment of agricultural practices has also resulted in machair degradation (i.e. a decline in floral diversity) in some areas, as a lack of management and grazing has led to the invasion of dominant grass species and scrub (Angus 2001; 'JNNC' 2010).

Large quantities of viable seed lies buried in soils and this 'seed bank' can potentially play a significant role in the restoration of plant communities following disturbance (Owen *et al*. 2001; Kalamees & Zobel 2002). However, changes to grassland management such as those described above can also have a significant impact on seed bank populations (Akinola *et al*. 1998; Sternberg *et al.* 2003; Bossuyt *et al*. 2006). The production of silage demands the use of fertilisers to promote the fast growth of grass species which, over time, out-compete the native species typical of unimproved grassland. As the presence of these native species in the vegetation is reduced, their representation in the soil seed bank also declines. Silage production allows grass crops to be harvested as early as May and June, before many wildflower species typical of unimproved grassland have set seed (Grime *et al*. 2007). This form of grassland management inevitably reduces the quantity of seed rain produced and consequently there is less seed available for incorporation into the soil seed bank. Similarly, intensive grazing of grassland habitats throughout the summer months can affect the composition of the seed bank by removing plant material before it has set seed. Conversely, in grassland swards that are dense and undisturbed (as is the case on abandoned crofts), opportunities for seed to reach the soil surface and become incorporated into the seed bank are low (Williams 1984).

The UK Biodiversity Action Plan for machair outlines the importance of researching methods with which to restore degraded areas of machair by manipulating the existing seed bank (UK Biodiversity Action Plan 2007). Using the existing seed bank would be preferable to importing seed mixes since these are likely to be of mixed provenance, which could potentially lead to a loss of locally-adapted races. The appropriate management and restoration of machair grassland is particularly important if this habitat is to continue supporting rare and declining species such as *B. distinguendus* (Goulson *et al*. 2006; ‘JNCC’ 2010). The principle aim of this research was to quantify the abundance of viable seed in the soil at machair sites across the Outer Hebrides (Scotland) and more specifically, to establish whether machair seed bank has the potential to provide a sufficient resource for reinstating the foraging resources required by rare and declining bumblebees, to degraded areas of machair. In addition, we assess whether the presence of dicotyledonous species in the seed bank can be predicted from their availability in the existing machair vegetation.

5.3 Methods

5.3.1 Seed bank sampling

Seed bank sampling is a notoriously time consuming process and most studies suggest that collecting a large number of small samples is preferable to collecting a few large samples, in order to accurately reflect all of the species present in the seed bank (Leck *et al*. 1989; Warr *et al*. 1993; Thompson *et al*. 1997). However, it has been suggested that taking between 15 and 20 samples will be sufficient to detect most of the species present in the seed bank of agricultural soils (Gross 1990). In order to maximise the efficiency of the sampling methodology and therefore increase the number of sites from which it was possible to sample, we first attempted to establish the minimum number of soil samples required in order to provide a representative list of the species present in the seed bank of machair.

Seed bank samples were collected from four machair sites on the Southern Hebridean Island of Oronsay. The four sites were selected on the basis that they encompassed a range of different land management practices including arable, permanent pasture and fallow. Forty samples were taken from within a 20m x 20m subsection of each machair site between the 3rd and 5th May 2007. The 20m x 20m plots were subdivided into $1m^2$ units numbered 1 to 400 and a random number table was used to generate 40 x $1m^2$ units from which a single, centrally positioned soil sample was taken. Samples consisted of a soil core collected using a soil corer with a diameter of 5.5cm. The seed which is most likely to contribute naturally to a plant community is that which is concentrated within the top 2-3cm of the soil profile but seed found at a depth of 5-10cm can also persist in the seed bank and can germinate following mechanical soil disturbance such as ploughing (Kalamees & Zobel 2002); therefore seed bank samples were taken to a depth of 10cm. A total volume of 9503 cm^3 soil was collected from an area of $950cm^2$ in each of the four machair areas.

Samples (n=160) were placed in individual polyethene bags and transported to the University of Stirling where they were then air dried in individual foil trays for a period of four weeks. Once dried, samples were sieved through a 0.5cm mesh sieve to remove any dried vegetation. Each sample was then placed in an individually labelled seed tray (23cm x 17.5cm x 11.5cm), on a bed of sterilised seedling compost approximately 5cm deep. Trays were randomly positioned outside in a gauze covered propagation tunnel to allow natural light and temperature fluctuation but also in order to avoid damage to the emerging seedlings by herbivores. Ten control trays containing only sterilised seedling compost were also arranged randomly amongst the sample trays in order to detect any compost or seed rain contamination from external sources. The seed trays were watered daily throughout the monitoring process.

5.3.2 Seedling emergence monitoring and species accumulation curves

As seedlings germinated they were identified to species level and removed from the seed trays. Any seedlings that were not immediately identifiable at this stage were removed from the seed trays and planted separately in plant pots until mature enough to be readily identified. Dicotyledonous species were identified to species level and all monocotyledonous species were grouped under a single category. Nomenclature of dicotyledonous species follows Stace (1997).

Species accumulation curves were generated using the random method (sub sampling without replacement) with 100 iterations and this was done in order to establish the minimum number of soil samples that would be required to detect the majority of species present in the seed bank. This and all subsequent analyses were conducted using the software package R (version 2.10.0, R Development Core Team 2009).

5.3.3 Extensive machair seed bank sampling

Based on the findings from the Oronsay samples (see results section), a total of 18 soil samples were collected from a further nine sites located across the three Outer Hebridean islands (fig. 5.1). The areas which were sampled were Bornish, South Uist (SU1), five sites around the Balranald area of North Uist (NU1, NU2, NU3, NU4, NU5), two sites at Northton and one site at Scarister on the Isle of Harris (HS1, HS2, HS3). Again, sites were selected because they encompassed areas of machair on which a range of land management practices, typical of current crofting activities, were implemented. These included cattle grazing, sheep grazing, silage production, arable cropping and fallow areas. Samples were taken during August 2008 and at each site samples were collected from within a 20m x 20m area, in accordance with the methodology used on Oronsay. A total of 4276.44 cm^3 soil was collected from a total area of 427.64cm^2 within each of the nine machair sites.

Soil samples were returned to the University of Stirling and processed as before. One hundred and sixty two seed trays containing the samples were randomly arranged within a gauze propagation tunnel and 14 control trays were set out. The trays were watered daily and emergent seedlings were identified and removed as before. Some studies of seed banks have stirred the soil regularly in order to expose seed and encourage germination (Milberg & Hansson 1993; Looney & Gibson 1995; Pakeman & Marshall 1997; Peco *et al*. 1998; Owen *et al*. 2001; Plassmann *et al*. 2009). For the purposes of this study, samples were not stirred during the monitoring process. This was done in order to mimic the effect of vegetative regeneration from the seed bank after a single human induced soil disturbance, e.g. ploughing. Any species identified from the control trays indicated that there was possible contamination from either seed rain or the compost and these species were excluded from analysis. It is worth noting that the two most abundant species observed in control trays during this experiment were *Chamerion angustifolium* and *Cardamine hirsuta*, neither of which is typically found in machair plant communities.

5.3.4 Vegetation sampling

In order to examine the relationship between the abundance of species in machair soil seed bank and the existing vegetation, eight of the nine machair sites described were also surveyed for dicotyledonous plant species. The ninth site was not included because it had been recently ploughed and there was no established vegetation to survey.

Surveying took place in April 2010; 18 months after the soil samples had been collected. This allowed any contribution of the seed bank to the existing vegetation, following annual disturbances cause by agricultural practices, to be recorded. At each of the sites, ten 0.5m x 0.5m quadrats were sampled from within the same 20m x 20m plots as the soil cores were taken and the percentage cover of each dicotyledonous plant species present was estimated. Nomenclature of species follows Stace (1997).

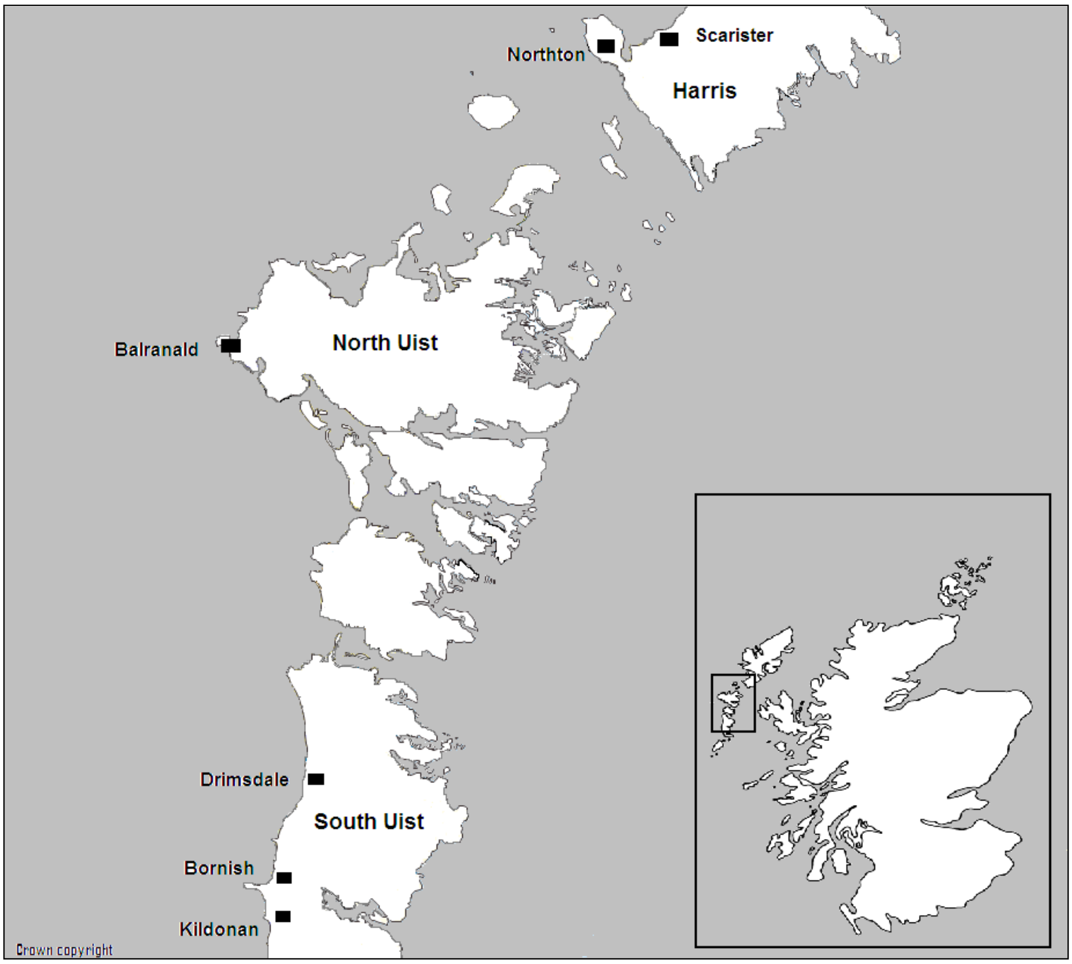

Figure 5.1: The location of sampling sites in the Outer Hebrides, including two sites, Drimsdale and Kildonan, which were previously sampled by Owen *et al*. (2001).

5.3.5 Data analysis

Replicate samples of the seed bank and vegetation for each site were pooled in order to give a single measure of abundance for each species, given as seeds m^{-2} and percentage cover m^{-2}, in the seed bank and vegetation respectively.

A Generalised Linear Mixed-Effects Model was used in order to examine whether the presence of dicotyledonous species in the seed bank can be predicted from their availability in the existing machair vegetation. Only samples containing a species present either in the vegetation surveys or the seed bank samples were used for the following analysis. Because of the high proportion of samples that did not contain seed for many species present in the vegetation (43% of 103 samples), the availability of each species in the seed bank was simply coded as present/absent and the model was run using binomial errors. The percentage cover of each plant species in the above ground vegetation was included in the model as a potential explanatory variable and site was included as a random factor. Plant species and whether the species was perennial, biennial or annual (according to Grime *et al*. 2007) were included in the model as fixed factors. All two- and three-way interactions were explored and non-significant interactions were removed sequentially using a backwards step-wise approach. An R^2 value was calculated to assess the fit of the model to the observed data.

5.4 Results

5.4.1 Seed bank - Oronsay

A total of 18 dicotyledonous plant species were recorded from samples taken across four sites on the Oronsay machair. Species accumulation curves for each of the four sites indicated that sampling 18 cores from a 20m x 20m area of machair will identify between 68% and 81% of species in the seed bank (fig. 5.2). The total species richness for each site was estimated by extrapolation of the species accumulation curves and this indicated that doubling the sampling effort would only increase the observed species richness by a mean of 2.34 species per site (Palmer 1990; Colwell *et al*. 1994).

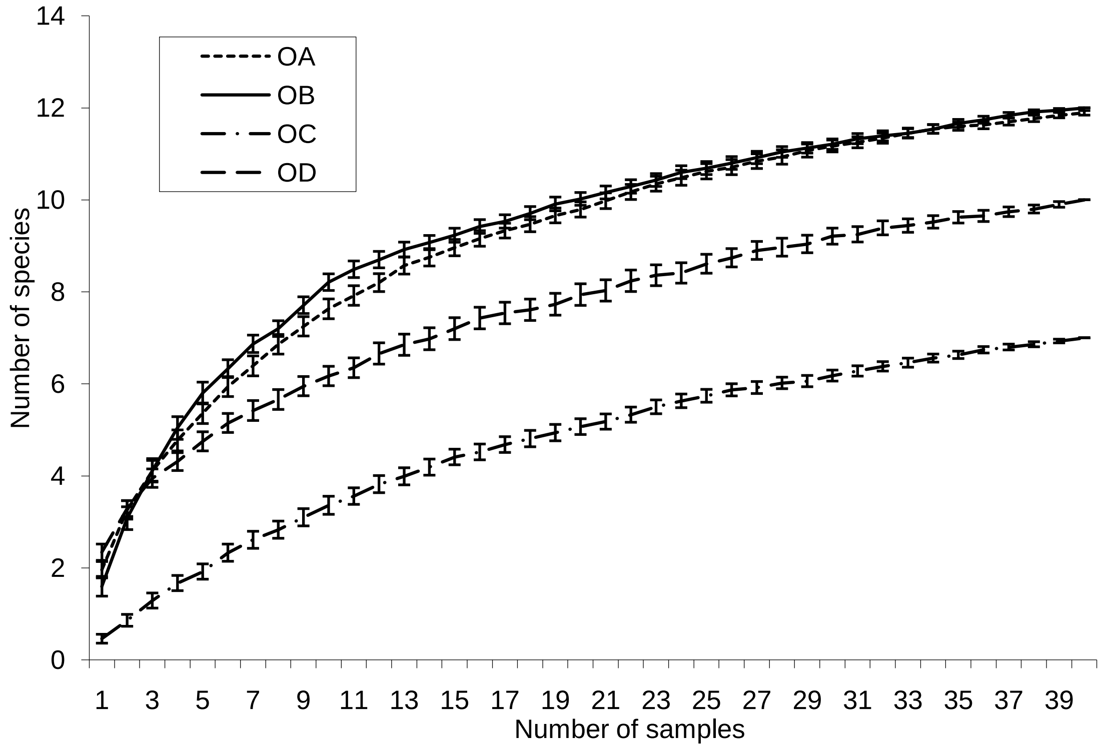

Figure 5.2: Species accumulation curves for seed bank samples collected at four sites, abbreviated to OA, OB, OC and OD, on the Island of Oronsay, Southern Hebrides.

5.4.2 The seed bank and vegetation - Outer Hebrides

A total of 431 seedlings comprising of 22 dicotyledonous plant species were recorded from the seed bank samples collected at nine machair sites across the Outer Hebrides. Of the species recorded, 11 were perennials, 10 were annuals and one was a biennial (table 5.1). The density of viable seeds (dicotyledonous species only) in the samples taken from each of the nine machair sites ranged from between 258 seeds m^{-2} and 1733 seeds m^{-2} (table 5.2). The mean density of viable seeds across all sites was 908 (± 158 SE) seeds m^{-2}.

Twelve of the species recorded in the seed bank were represented by fewer than five seedlings in total. The most abundant species in the seed bank was *Ranunculus acris,* which was observed in samples collected from all nine machair sites. *Bellis perennis* was observed in the seed bank of all but one of the sites and both *Plantago lanceolata* and *Leontodon autumnalis* were found in samples from six of the nine sites. *Prunella vulgaris* was observed in samples from five of the sites.

A total of 23 dicotyledonous species were recorded in the above ground vegetation at eight machair sites, a similar number to that found in the seed bank. The number of annual, perennial and biennial species recorded in the above ground vegetation across all sites was seven, fourteen and two respectively (table 5.1). Fifteen of the dicotyledonous species observed were found in both the seed bank and the vegetation and eight species were found in the vegetation only (table 5.1). Therefore, seven of the species recorded in the seed bank samples were not observed in the above ground vegetation (table 5.1).

5.4.3 Comparison of the seed bank and vegetation

The effect of percentage cover vegetation on the presence of that species in the seed bank varied according to whether the species was a perennial, annual or biennial (z = 2.27, p = 0.0260). However, the proportion of the variation explained by this model was small (R^2 = 9.8%). Only two annual species occurred in both the above ground vegetation and the seed bank, whilst six of the perennial species recorded, occurred in both the vegetation and the seed bank samples.

Table 5.1: The species present in the seed bank and vegetation at nine machair sites in the Outer Hebrides. Shaded rows indicate species known to be utilised by foraging bumblebees on machair grassland (Charman 2007; Redpath *et al*. 2010).

Species		**Site**								
		NU1	NU2	NU3	NU4	NU5	SU1	HS1	HS2	HS3
Annual										
	Chenopodium album									■
	Erodium cicutarium				■□		□			
	Euphrasia officinalis				□	□	□	■		
	Geranium molle				□		□			
	Linum catharticum			■		■	■	■	■	
	Myosotis arvensis			■					■	
	Papaver rhoeas				■		■			
	Persicaria maculosa	□								
	Rhinanthus minor	■			□	□				
	Sonchus asper			■						
	Stellaria media								□	□
	Valerianella locusta			■	■					■
	Veronica arvensis	■		■			■			■□
Perennial	*Achillea millefolium*		□		□	□	□			□
	Anthyllis vulneraria				□	□				
	Bellis perennis	■□	■□	■	□	■□	■□	■□	■□	■□
	Calystegia sepium			■						
	Cerastium fontanum	□		■	■□	□	□		■□	□
	Iris pseudacorus							□		
	Leontodon autumnalis		□	■	■□	■□	■□	■□	■	■□
	Lotus corniculatus						□	■		
	Plantago lanceolata	■□	■		□	■□	■□	■□	■□	■□
	Potentilla anserine		□							
	Prunella vulgaris	■□	■		□	□	■□	■	■	□
	Ranunculus acris	■□	■□	■	■□	■□	■□	■□	■□	■□
	Rumex acetosa		□		■				□	□
	Rumex obtusifolius		□							■
	Trifolium repens	□	□	■	□	□	□	□	□	□
Biennial	*Senecio jacobaea*				■□	■□	■□		■□	
	Heracleum sphondylium					□			□	

■ = species present in seed bank □ = species present in the vegetation

Table 5.2: The composition and density of the species present in the soil seed bank at nine machair sites in the Outer Hebrides. Shaded rows indicate species known to be utilised by foraging bumblebees on machair grassland (Charman 2007; Redpath *et al*. 2010).

Species	**Number of seeds m^{-2}**								
	NU1	NU2	NU3	NU4	NU5	SU1	HS1	HS2	HS3
Chenopodium album	0	0	0	0	0	0	0	0	23.4
Erodium cicutarium	0	0	0	23.4	0	0	0	0	0
Euphrasia officinalis	0	0	0	0	0	0	46.8	0	0
Linum catharticum	0	0	23.4	0	93.7	46.8	70.3	70.3	0
Myosotis arvensis	0	0	23.4	0	0	0	0	234.2	0
Papaver rhoeas	0	0	0	46.8	0	23.4	0	0	0
Rhinanthus minor	23.4	0	0	0	0	0	0	0	0
Sonchus asper	0	0	23.4	0	0	0	0	0	0
Valerianella locusta	0	0	257.6	70.3	0	0	0	0	23.4
Veronica arvensis	46.8	0	70.3	0	0	46.8	0	0	281.0
Bellis perennis	163.9	23.4	70.3	0	140.5	70.3	117.1	23.4	46.8
Cerastium fontanum	0	0	23.4	23.4	0	0	0	70.3	0
Leontodon autumnalis	0	0	117.1	515.2	46.8	163.9	93.7	93.7	0
Lotus corniculatus	0	0	0	0	0	0	163.9	0	46.8
Plantago lanceolata	23.4	117.1	0	0	117.1	398.1	281	93.7	0
Potentilla anserina	0	0	0	0	0	0	0	0	23.4
Prunella vulgaris	140.5	23.4	0	0	0	187.4	749.4	70.3	0
Ranunculus acris	445.0	93.7	93.7	46.8	655.7	772.8	93.7	398.1	93.7
Rumex acetosa	0	0	0	46.8	0	0	0	0	0
Rumex obtusifolius	0	0	0	0	0	0	0	0	23.4
Trifolium repens	0	0	23.4	0	0	0	0	0	0
Senecio jacobaea	0	0	0	23.4	23.4	23.4	0	46.8	0
*Total	843	258	749	796	1077	1733	1616	1101	562

*To nearest whole number.

5.5 Discussion

5.5.1 Machair seed bank

The machair seed bank samples collected during this study, from a number of locations in the Outer Hebrides, demonstrate a seed bank density that ranges from between 258 to 1733 seeds m^{-2}. This seed bank density is much greater than previously described for machair soils. Owen *et al*. (2001) looked at the spatial and temporal variability of machair seed banks and found the range of seed densities to be between 7 and 58 seeds m^{-2}. Although, the authors took soil samples to a shallower depth (4cm) than the samples collected during this research (10cm), the majority of seed is likely to be concentrated in the upper most layers of the soil profile and this difference is unlikely to have resulted in the dissimilarity observed between the two machair studies.

The mean density of the machair seed bank data presented here (908 seeds m^{-2}) is comparable with grassland habitats elsewhere in Europe (Bossuyt *et al.* 2006). Research in Belgium, which assessed the potential of calcareous grassland habitats to be restored from the existing seed bank after a period of abandonment, found a mean seed density of 930 seeds m^{-2}. The authors also found, similarly to this study, that the most abundant species in the seed bank were common species, typical of species-poor grasslands (Bossuyt *et al.* 2006). The total number of species recorded here, across all nine study sites, was comparable to the number of species found in other studies which have looked at the seed bank of agricultural soils (e.g. Owen *et al*. 2001; Boguzas *et al*. 2004).

Although the evidence outlined here, suggests that the soil seed bank is greater than previously thought (Owen *et al*. 2001), the species composition of the seed bank will also be important if bumblebee foraging habitat is to potentially be created as a result of seed bank manipulation. During this study, some plant species that are characteristic of machair vegetation were not found in the seed bank samples. In particular, common knapweed (*Centaurea nigra)* and red clover (*Trifolium pratense)* are two species that were absent from the seed bank samples but which are characteristic of machair grassland vegetation (Kent *et al*. 2003). These species, in conjunction with a small number of other native wildflowers, form a suite of forage plants which are utilised by *B. distinguendus* and it is their availability within machair grasslands that has resulted in the strong association between the habitat and this rare *Bombus* species (Charman 2007; Redpath *et al*. 2010).

The lack of *C. nigra* seeds in the seed bank samples is to be expected as this species does not generally have a persistent seed bank, and although some seeds may survive for a period of several years, this species typically sheds its seed in the autumn and winter with germination taking place during the following spring (Grime *et al*. 2007). As the seed bank samples collected during this research were taken during the summer, any *C. nigra* present in the vegetation would not have set seed yet and therefore detecting this species during seed bank sampling would have been unlikely. In contrast to *C. nigra*, *T. pratense* is reported to have a persistent seed bank and typically sets seed in July with germination occurring in the autumn (Grime *et al*. 2007). Therefore, this species could reasonably have been expected to occur in the seed bank samples and its absence would suggest that the seed bank of the machair sites sampled does not contain a significant quantity of *T. pratense* seed.

Despite the lack of these two key forage plants in the seed bank, five species known to provide forage material for *B.distinguendus* on machair habitats were detected in the seed bank samples (tables 5.1 & 5.2). *Trifolium repens*, *Lotus corniculatus* and *Prunella vulgaris* were all recorded in the seed bank samples and are typical of machair plant communities (Kent *et al*. 2003). *Rhinanthus minor* was detected in the seed bank samples collected from one site (table 5.1) but this is likely to have been an anomaly as this species does not form a persistent seed bank and is instead dependant on annual seed production in order to regenerate and persist in grassland habitats (Grime *et al*. 2007). Therefore, we would not have expected this species to occur during seed bank sampling and any *R. minor* seedlings recorded during this study are likely to have been the result of accidental contamination during preparation of the seed trays. The fifth bumblebee forage plant species to be recorded in the seed bank samples was *Senecio jacobaea* but whilst this species is utilised by foraging bumblebees, including *B.distinguendus*, it would be inappropriate to promote this species as an element of any bumblebee habitat creation, particularly within agricultural landscapes, as it is highly toxic to livestock (Grime *et al*. 2007).

Grassland species are often relatively short lived in the seed bank and it is common in grassland habitats for there to be little correspondence between the species which occur in the seed bank and those which occur in the vegetation and machair appears to be no exception (Milberg & Hansson 1993; Warr *et al*. 1993; Bakker & Berendse 1999). Although some perennial species occurred frequently in both the vegetation and the seed bank (e.g. *R. acris* and *B. perennis*), there were several species observed in the above ground vegetation that were not represented in the seed bank and vice versa.

5.5.2 The importance of machair restoration

For at least the last 2000 years, machair in the Outer Hebrides has undergone periods of agricultural use (Ritchie 1967). Machair habitats have become fundamentally linked with the crofting practices that take place on and around them. Machair grassland plant communities have been influenced and maintained by rotational cultivation, grazing practices and the use of kelp to trap moisture, fertilize soils and to stabilise the light sandy surface soils typical of machair (Kent *et al*. 2003). Unfortunately, more intensive agricultural practices are beginning to replace these traditional regimes, with over grazing leading to reduced sward diversity in some areas and complete agricultural abandonment and subsequent lack of grazing resulting in rank grassland vegetation, low in plant species diversity, in other areas (Kent *et al*. 2003).

In conclusion, this study supports the existing body of evidence which suggests that the restoration of grassland habitats is unlikely to be successful if it is to rely entirely on the existing seed bank. This research has established that there is some correspondence between the availability of a species in the above ground machair vegetation and its presence in the seed bank. However, plant species differ in their persistence within the seed bank and therefore, just because a species is present in the vegetation of machair grassland does not mean we can assume that it will occur in the seed bank. This suggests, in combination with the fact that key bumblebee forage plant species, typical of machair grassland were absent from the seed bank, that additional seed input from external sources is likely to be required in order to re-create wildflower-rich machair habitat (Muller *et al*. 1998; Reiné *et al*. 2004). This will be particularly important if machair grassland is to be restored in order to provide high quality foraging habitat for rare bumblebees, as some of the perennial species on which they rely were absent from the machair seed bank. Although the cost of implementing wildflower-rich seed mixes can prove to be expensive (see chapter 6 of this thesis), the cost of restoration could be reduced by disturbing the soil and adding only seed of those species such as *C. nigra* and *T. pratense*, which are known to be largely absent from the existing seed bank.

6 Restoration and management of machair grassland for the conservation of bumblebees

6.1 Abstract

Machair is a rare coastal grassland habitat, listed on the EU Habitats Directive, which supports populations of nationally and internationally rare species including the bumblebee species, *Bombus distinguendus* and *Bombus muscorum*. However, changes in traditional land management practices have resulted in a loss of floral diversity in some areas which has, in turn, reduced the availability of bumblebee foraging resources. A restoration trial was established on a degraded machair site in western Scotland and comprised four seed mixes and a fallow treatment which were monitored over a three year period (2008-2010), in order to compare the relative abundance of foraging bumblebees and the availability of forage plants. Two seed mixes contained wildflower species identified as key bumblebee forage plants; one mix is currently used to create bird and bee foraging habitat on nature reserves and the fourth mix is a commercially available mix used for reseeding pasture. There was little variation in forage availability and bumblebee abundance between treatments early on each year (i.e. June 2008, 2009 and 2010) but marked differences emerged later in the season in all three years. By the end of the monitoring period (August 2010), the two wildflower treatments contained between four and eighteen times the number of inflorescences than any other treatment type. Similar trends were observed in bumblebee abundance, reflecting the availability of floral resources. Some of the rarest bumblebee species exist primarily in restricted areas, which have largely escaped the intensification typical of mainstream farming. In these areas it is important that habitat management is specifically targeted and translated into appropriate agri-environment schemes. We

suggest that the most effective method for restoring bumblebee forage plants on machair is to sow wildflower-rich seed mixes which ensure the provision of forage material throughout the season. The use of these mixes should be combined with late cutting and winter grazing practices to maintain machair sward diversity over time.

6.2 Introduction

Machair is one of Europe's rarest habitats. It is limited in its global distribution to the north and west of Scotland and Ireland and is listed on the EU Habitats Directive (Angus 2001; Love 2003). Machair is described as a low-lying coastal grassland habitat which forms on lime-rich soils comprising largely of blown sand, rich in shell derived material (Ritchie 1967; Angus 2001; Love 2003).

Scottish machair supports nationally and internationally important populations of several species. To date, research has largely focused on the importance of machair for avian species, including corn bunting (*Emberiza calandra*), twite (*Carduelis flavirostris*), corncrake (*Crex crex*), lapwing (*Vanellus vanellus*), redshank (*Tringa totanus*), dunlin (*Calidris alpina*) and ringed plover (*Charadrius hiaticula*) (Wilson 1978; Jackson & Green 2000; Wilson *et al.* 2007; Wilkinson & Wilson 2010). However, a number of invertebrate species including the UK Biodiversity Action Plan (UKBAP) priority species, the great yellow bumblebee (*Bombus distinguendus*) and the moss carder bumblebee (*Bombus muscorum*), are also particularly associated with the florally rich machair grassland of the Inner and Outer Hebridean islands (Benton 2006; Goulson *et al*. 2006; Beaumont & Housden 2009).

Bumblebees have undergone substantial declines in recent decades and of the 25 *Bombus* species native to the UK, three have gone extinct and several of the remaining species are severely threatened (Goulson 2003a). Agricultural intensification has been held largely responsible for the decline of many species associated with farmland and bumblebees are no exception (Chamberlain *et al*. 2000; Goulson 2003a; Goulson *et al.* 2008a).

The land management practices that have traditionally been implemented on machair include low intensity grazing and rotational cropping and these crofting practices are fundamentally linked to the floral diversity for which machair grassland habitats are renowned (Roberts *et al.* 1959; Ritchie 1967; Owen *et al*. 2001; Kent *et al*. 2003). However, the increasing modernisation, or conversely in some cases, the abandonment of traditional crofting practices, has led to machair degradation (i.e. a decline in floral diversity) in many areas (Angus 2001; Hansom & Angus 2005; Redpath *et al*. 2010). This in turn is likely to have an impact on the species that currently thrive on machair and in particular, the loss of florally rich machair swards poses a very real threat to remaining populations of the UK's rarest bumblebee species.

This study examines the efficacy of five different machair restoration treatments in providing foraging habitat for bumblebees on an area of degraded machair on the southern Hebridean island of Oronsay. The principle aim of this research is to identify the most effective treatment or treatments for restoring floral diversity to an internationally rare habitat in order to provide resources for rare and declining *Bombus* species.

6.3 Methods

6.3.1 Study site

The island of Oronsay lies to the south west of the larger neighbouring island of Colonsay, which is situated 32km west of the Scottish mainland. The area of machair that was selected for this study had been heavily grazed by sheep for more than a decade and consequently lacked floral diversity. A rotational cropping regime was implemented at the site three years prior to the start of this experiment using oats, rye and barley. This change in land management practice was an attempt to restore traditional land management practices to the machair. However, like many crofts which continue to be actively managed, inorganic fertilizer (NPK 16:10:10) was applied annually at a rate of 500kg/ha, replacing the use of the traditional fertilisers such as seaweed or farmyard manure.

6.3.2 Restoration treatments

In March 2007 the machair was ploughed and the ground prepared by adding a single application of both agricultural lime and farmyard manure. Seaweed could not be used on Oronsay as the island is a designated Special Protection Area (SPA) for red-billed chough (*Pyrrhocorax pyrrhocorax*) and seaweed that is washed ashore is left on the beaches to provide the choughs with suitable foraging habitat.

In May 2007 the site was divided in to 25 plots, each with a total area of 125m^2 (5m x 25m). Five machair restoration treatments were implemented (table 6.1), each with five replicates and the treatment plots were arranged in a quasi-complete Latin square design so that each treatment type was adjacent to every other treatment type at least once. This design also minimises the impact of variation in soil quality across the site. As would have been traditional on cultivated machair, a fast growing nurse crop of oats and bere barley was sown over the treatments to protect the wildflower seedlings in the early stages of growth and also to aid the stabilisation of the light, sandy soil (Roberts *et al*. 1959). At the end of the first year (2007) the site was not cut or grazed in order to allow the young plants to establish. In the second, third and fourth years of this study, the treatments were cut and baled as silage in early September. Livestock in the form of both cattle and sheep were put on to aftermath graze the site between September and mid March. This system of rotational cutting and grazing is in accordance with traditional crofting practice.

6.3.3 Vegetation surveys

The availability of bumblebee forage material in each of the 25 plots was monitored in June, July and August over a three year period, from 2008 to 2010. Six 0.5m x 0.5m quadrats were positioned at regular intervals in each plot, along a central transect line, and the number of inflorescences of each bumblebee forage plant species present was recorded. Bumblebee forage plant species were defined as the species known to be utilised by bumblebees foraging on machair sites in western Scotland, as described by Charman (2007) and Redpath *et al*. (2010).

6.3.4 Bumblebee surveys

In addition to monitoring the presence of forage plant species, each plot was also surveyed for the presence of foraging bumblebees. Similarly to the vegetation surveys, each plot was monitored in June, July and August throughout the three year period (2008-2010). Each plot was surveyed for bumblebees twice, once in the morning and once in the afternoon, and the total number of bees observed in each plot across the two surveys was summed to give a single figure. The treatments were not surveyed for the presence of foraging bumblebees in the first year (2007) in order to allow seedlings to become established and to allow perennial species to flower.

A standard surveying methodology, adapted from Pollard (1977), was used to record observations of foraging bumblebees. A transect was walked at a constant speed through the centre of each plot, each walk taking an average of about five minutes. All bumblebees observed foraging either side of the transect line, but within the plot area, were recorded and identified to species level and all castes were combined. The plant species on which bees were observed foraging were also recorded.

6.3.5 Data analysis

The availability of forage plant material (the number of inflorescences) in each restoration treatment plot was examined using a generalised linear mixed effects model (GLMM) with Poisson errors in the software package R version 2.10.1 (R Development Core Team 2009). Treatment type, month and year were included in the model as fixed factors and plot number was included as a random factor. All two- and three-way interactions were explored and non-significant interactions were removed sequentially using a backwards step-wise approach. Pair-wise post hoc comparisons were conducted, using Tukey tests in the Multcomp package in R version 2.10.1, in order to assess differences in forage availability among treatment types in each month and in each year.

The effect of machair restoration treatment on the abundance of foraging bumblebees was also examined using a generalised linear mixed effects model with Poisson errors. The availability of inflorescences was included in the model as an explanatory variable and treatment type, month and year were included in the model as fixed factors. Plot number was also included in the model as a random factor. All two- and three-way interactions were explored and non-significant interactions were removed sequentially using a backwards step-wise approach. Pair-wise post hoc comparisons were conducted, as before, using the Multcomp package in R, in order to assess the differences in bumblebee abundances between treatment types in each month. A pseudo R^2 value (hereafter referred to as R^2 values) was calculated for each GLMM, by correlating the values predicted by each model with the observed data (Zuur *et al.* 2009).

Table 6.1: Five machair restoration treatments and their definitions (prices accurate for 2010 and inclusive of VAT)

Treatment Type	Cost of Seed (£/kg)	Sowing Rate (kg/ha)	Total Cost (£/ha)	Definition
1. Wildflower 1	63.00	30.00	1890.00	Grass seed mixture containing plant species native to machair habitats but also known to be of importance for foraging bumblebees (ratio grass to wildflowers 80:20). These species were as follows: *Lotus corniculatus, Arctium minus, Prunella vulgaris, Rhinanthus minor, Trifolium pratense, Trifolium repens, Vicia cracca, Succisa pratensis, Thymus polytrichus, Cynosurus cristatus, Alopecurus pratensis, Festuca rubra ssp litoralis, Poa pratensis*
2. Wildflower 2	200.00	20.00	4000.00	Wildflower 1, minus the grass species
3. Bird & Bee conservation	4.00	6.17	24.68	A brassica rich mix already implemented elsewhere in the Hebrides for the conservation of birds but with added clover and phacelia to encourage foraging bumblebees. The mix contained kale, mustard, phacelia, fodder radish, linseed and red clover.
4. Commercial	4.50	29.65	133.43	A commercially available grass mix for re-seeding pasture. The mix contains approximately 5% white clover, an important bumblebee forage plant.
5. Fallow	N/A	N/A	N/A	The ground was ploughed and no seed was added. The vegetation was left to regenerate naturally from the existing seed bank.

6.4 Results

6.4.1 Bumblebee forage plant availability

The relationship between the availability of bumblebee forage plant material and treatment type was influenced significantly by both month and year, and both of these factors interacted with treatment type (table 6.2). For this reason the pair wise comparisons for forage plant availability in different treatment types were examined separately for each year (tables 6.3, 6.4 and 6.5). The model explained 66% of the variation observed within the dataset.

In June 2008 there were relatively few flowers in any of the plots. There were significant differences between 'Fallow' plots and the 'Bird & Bee,' 'Wildflower 1' and 'Wildflower 2' treatments, with 'Fallow' plots containing, on average, twice as many inflorescences (based on the median number of inflorescences per treatment). The only other significant difference between treatments occurred between the 'Commercial' treatment and both 'Wildflower 1' and the 'Bird & Bee' treatments. In both cases, the 'Commercial' treatment held on average twice as many inflorescences. Later in the same year (July and August), the two wildflower treatments contained significantly more inflorescences than any of the other treatment types, with differences between wildflower and non-wildflower treatments ranging from two to seven times more flowers (table 6.3, fig. 6.1a).

In June 2009, the only significant differences in inflorescence availability were between the 'Wildflower 2,' 'Commercial' and 'Fallow' treatments and the 'Bird & Bee' mix. The former three treatments demonstrated between one and a half and three times the number of bumblebee forage plant inflorescences than the 'Bird & Bee' treatment. In July and August 2009, the differences between treatments were very similar to those observed in 2008 with the exception of the 'Commercial' treatment, which was no longer significantly different from the 'Wildflower 1' treatment (table 6.4, fig. 6.1b).

In June 2010, the 'Wildflower 1' treatment plots contained significantly more inflorescences than any other treatment type (table 6.5, fig. 6.1c). The following month, differences between treatments became more varied. 'Wildflower 1'and 'Bird & Bee' treatments provided more inflorescences than either the 'Commercial' or 'Fallow' treatments. 'Wildflower 2' treatment plots provided more inflorescences than the 'Commercial' treatment only. However, by August 2010 the pattern of floral abundance reflected those observed in the same month in both 2008 and 2009. The two wildflower treatments held significantly more bumblebee forage plant inflorescences than any other treatment type, providing between four and fifteen times more inflorescences than the 'Fallow', 'Commercial' or 'Bird & Bee' treatments.

The 'Bird & Bee' treatment included *Trifolium repens* and *Trifolium pratense,* both commonly utilized bumblebee forage plant species, but this treatment contained much lower numbers of *T. pratense* inflorescences when compared with the two wildflower treatments. Throughout the survey period there were between four and twenty times more *T. pratense* inflorescences per $0.5m^2$ quadrat in the wildflower treatments than in the 'Bird and Bee' treatment.

The commercial grass seed treatment only included one forage plant species, *T. repens,* but another forage plant species, *Odontites verna,* was commonly recorded in this treatment during the second year of the study. Whilst bumblebees will forage on this species, fewer than five percent of foraging visits were to *O. verna* (table 6.6). The fallow treatment plots were dominated by *T. repens* in the first and second year and they demonstrated little variation in floral abundance throughout the months.

Overall, *T. repens* was the most commonly available forage plant in June with more than 67% of the available inflorescences belonging to this species. In July *T. repens* and *O. verna* were the most abundant forage plants with 33% and 20% of available inflorescences belonging to these two species respectively. *Trifolium pratense* became the most commonly available forage plant in August, contributing 63% of the total inflorescence availability.

Table 6.2: A summary of test statistics derived from the models examining the effect of machair restoration treatments, month and year on the abundance of foraging bumblebees and their forage plant inflorescences on an area of machair, Isle of Oronsay (*p=<0.05, **p=<0.01, ***p=<0.001).

	Inflorescences	**Bumblebees**
Year	N/A	χ^2= 241.50***
Inflorescence	N/A	χ^2 = 23.97***
Treatment:Month	χ^2 = 591.30***	χ^2 = 230.28***
Treatment:Year	χ^2 = 302.11***	N/S

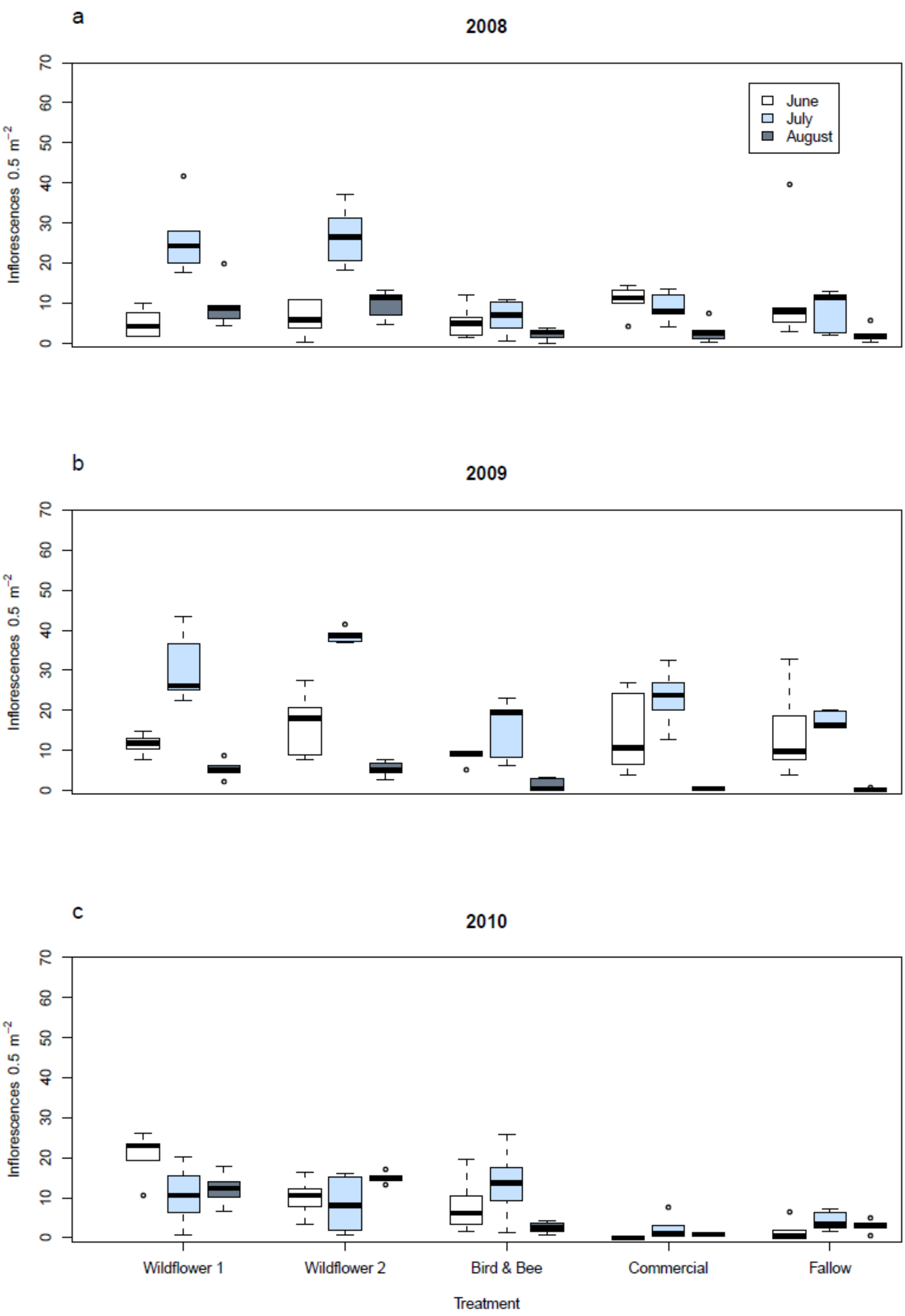

Figure 6.1: a-c Box plots showing the abundance of bumblebee forage plant inflorescences observed on five different machair restoration treatments across three consecutive months (June, July, and August) in three consecutive years. The boxes represent the median and the 25-75% quartile range.

Table 6.3: Pair wise comparisons for the effect of machair restoration treatment type on the abundance of bumblebee forage plant material across the months of June, July and August in 2008 following a GLMM which indicated the significant interacting effect of treatment type and month. Negative t values indicate that the treatment types listed along the rows of the table had fewer available inflorescences than the treatment types listed in the columns. Bold font indicates which comparisons are statistically significant (*p=<0.05, **p=<0.01, ***p=<0.001).

Month	**Treatment Type**	**Wildflower 1**		**Wildflower 2**		**Bird & Bee Mix**		**Commercial Mix**	
		z	p	z	p	z	p	z	p
June	Wildflower 2	0.860	0.909						
	Bird & Bee Mix	0.253	0.999	-6.09	0.973				
	Commercial Mix	**3.108**	*****	2.327	0.133	**2.886**	*****		
	Fallow	**4.007**	*******	**3.283**	*******	**3.803**	******	1.028	0.839
July	Wildflower 2	0.133	1.000						
	Bird & Bee Mix	**-7.131**	*******	**-7.226**	*******				
	Commercial Mix	**-6.218**	*******	**-6.325**	*******	1.396	0.618		
	Fallow	**-6.524**	*******	**-6.628**	*******	0.971	0.862	-0.432	0.992
August	Wildflower 2	-0.016	1.000						
	Bird & Bee Mix	**-4.416**	*******	**-4.404**	*******				
	Commercial Mix	**-4.088**	*******	**-4.076**	*******	0.569	0.978		
	Fallow	**-4.451**	*******	**-4.440**	*******	-0.071	0.999	-0.639	0.966

Table 6.4: Pair wise comparisons for the effect of machair restoration treatment type on the abundance of bumblebee forage plant material across the months of June, July and August in 2009 following a GLMM which indicated the significant interacting effect of treatment type and month. Negative t values indicate that the treatment types listed along the rows of the table had fewer available inflorescences than the treatment types listed in the columns. Bold font indicates which comparisons are statistically significant (*p=0.05, **p=0.01, ***p=<0.001).

Month	Treatment Type	Wildflower 1		Wildflower 2		Bird & Bee Mix		Commercial Mix	
		z	p	z	p	z	p	z	p
June	Wildflower 2	2.102	0.217						
	Bird & Bee Mix	-1.559	0.521	**-3.573**	**				
	Commercial Mix	1.284	0.699	-0.832	0.920	**2.799**	*		
	Fallow	1.325	0.673	-0.791	0.932	**2.838**	*	0.041	1.000
July	Wildflower 2	2.115	0.2102						
	Bird & Bee Mix	**-4.935**	***	**-6.810**	***				
	Commercial Mix	-2.275	0.150	-4.330	***	**2.783**	*		
	Fallow	**-4.145**	***	-6.089	***	0.866	0.907	-1.939	0.2928
August	Wildflower 2	0.021	1.000						
	Bird & Bee Mix	**-3.098**	*	**-3.113**	*				
	Commercial Mix	**-3.586**	**	**-3.591**	**	-1.413	0.588		
	Fallow	**-3.474**	**	**-3.482**	**	-1.725	0.386	-0.476	0.987

Table 6.5: Pair wise comparisons for the effect of machair restoration treatment type on the abundance of bumblebee forage plant material across the months of June, July and August in 2010 following a GLMM which indicated the significant interacting effect of treatment type and month. Negative t values indicate that the treatment types listed along the rows of the table had fewer available inflorescences than the treatment types listed in the columns. Bold font indicates which comparisons are statistically significant (**p*=<0.05, ***p*=<0.01, ****p*=<0.001).

Month	**Treatment Type**	**Wildflower 1**		**Wildflower 2**		**Bird & Bee Mix**		**Commercial Mix**	
		z	p	z	p	z	p	z	p
June	Wildflower 2	-4.105	***						
	Bird & Bee Mix	-4.902	***	-0.937	0.858				
	Commercial Mix	-3.317	**	-2.900	*	-2.784	*		
	Fallow	-6.983	***	-4.736	***	-4.120	***	1.884	0.277
July	Wildflower 2	-1.190	0.748						
	Bird & Bee Mix	1.268	0.700	2.428	0.102				
	Commercial Mix	-4.569	***	-3.677	**	-5.431	***		
	Fallow	-3.627	**	-2.574	0.070	-4.667	***	1.357	0.644
August	Wildflower 2	1.198	0.731						
	Bird & Bee Mix	-5.090	***	-5.854	***				
	Commercial Mix	-5.377	***	-5.862	***	-1.765	0.367		
	Fallow	-4.918	***	-5.728	***	0.349	0.996	2.055	0.218

6.4.2 Bumblebee species

A total of 411 foraging bumblebees, belonging to six species, were observed throughout the survey period (table 6.6). *Bombus hortorum* was the most commonly observed species overall followed by the UK Biodiversity Action Plan priority species, *B. muscorum*. *Bombus campestris* was only recorded in August 2009, the first time that this species had been recorded on the island. Although *B. distinguendus* is strongly associated with machair habitats this species does not occur on the island of Oronsay and was therefore not observed during this study. In all three years bumblebee abundance was highest in August with a total of 61% of all observations of foraging bumblebees occurring in this month.

Table 6.6: The percentage of each bumblebee species (total *n*=411) observed foraging across all treatment types and across all years (2008-2010).

Bumblebee Species	**% Total Bumblebees**
B. hortorum	33.58
B. muscorum	30.66
B. lucorum	18.49
B. pascuorum	12.65
B. jonellus	4.38
B. campestris '*swynnertoni*'	0.24

6.4.3 Machair restoration treatment type and bumblebee abundance

Bumblebee numbers were highest in 2008 (n=259) followed by 2009 (n=133) but numbers were very low in 2010 with only 19 bees observed. The relative abundances of foraging bumblebees across the five different treatment types, however, remained broadly similar across all years (figs.6.2a-c).

The observed number of bees per plot varied significantly between months, years and treatment type, and the effect of month (but not year) on bumblebee abundance differed between the treatment types (table 6.2). There were no significant differences between the number of foraging bumblebees on treatments in June or in July. However, differences were observed between treatments in August (fig 6.2a-c, table 6.7). Overall this model explained 84% of the variation in the observed bumblebee abundances.

Both 'Wildflower 1' and 'Wildflower 2' treatments attracted significantly higher numbers of foraging bumblebees than all other treatments in August. There were no significant differences between the number of bees observed on the two wildflower treatments in any month, and this held for the three years of the study (table 6.7). The differences in bumblebee abundance between treatments was most pronounced in August when between three and nine times more bees were observed foraging on the two wildflower treatments than on any other treatment type. In comparison, there were relatively small differences between the numbers of bees observed on the non-wildflower treatments (fig.6.2 a-c).

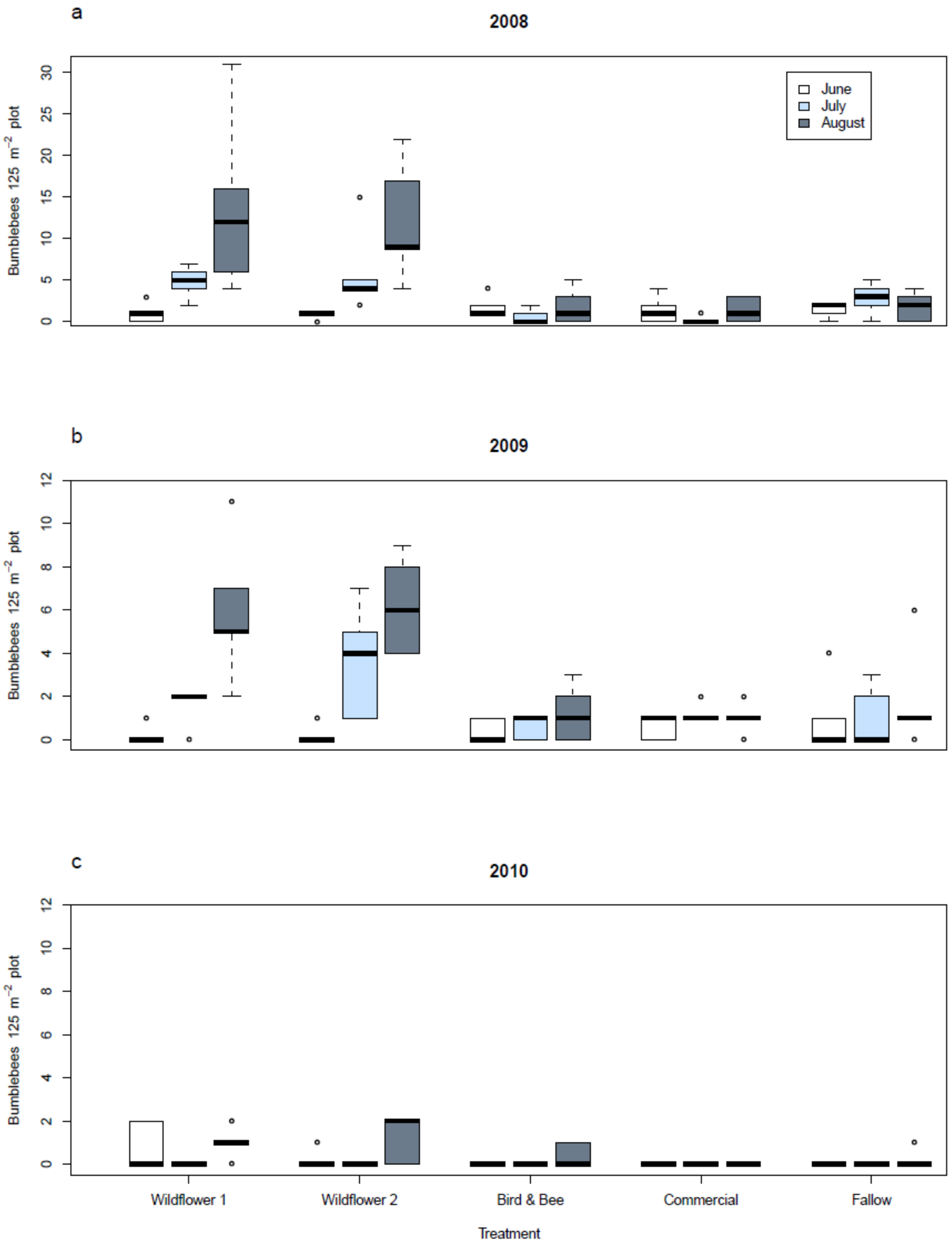

Figure 6.2: a-c Box plots showing the abundance of bumblebees observed foraging on five different machair restoration treatments across three consecutive months (June, July, and August) in three consecutive years. The boxes represent the median and the 25-75% quartile range. Note the difference in scale on the y-axis between 2008 and 2009-10.

Table 6.7: Pair wise comparisons for the effect of machair restoration treatment type on the abundance of foraging bumblebees across the months of June, July and August over a three year period following a GLMM which indicated the significant interacting effect of treatment type and month. Negative z values indicate that the treatment types listed along the rows of the table attracted fewer foraging bumblebees than the treatment types listed in the columns. Bold font indicates which comparisons are statistically significant (**p*=<0.05, ***p*=<0.01, ****p*=<0.001).

Month	**Treatment Type**	**Wildflower 1**		**Wildflower 2**		**Bird & Bee Mix**		**Commercial Mix**	
		Z	p	z	p	z	p	z	p
June	Wildflower 2	-0.139	0.836						
	Bird & Bee Mix	0.339	0.997	1.344	0.662				
	Commercial Mix	-0.140	1.000	0.917	0.890	-0.477	0.989		
	Fallow	0.057	1.000	1.097	0.807	-0.273	0.999	0.203	1.000
July	Wildflower 2	0.925	0.880						
	Bird & Bee Mix	-1.058	0.818	-1.501	0.546				
	Commercial Mix	-1.376	0.628	-1.833	0.311	-0.164	1.000		
	Fallow	1.004	0.845	0.420	0.993	2.116	0.201	2.420	0.103
August	Wildflower 2	-0.078	0.999						
	Bird & Bee Mix	**-3.624**	**	**-3.602**	**				
	Commercial Mix	**-4.094**	***	**-4.075**	***	-0.705	0.954		
	Fallow	**-3.267**	**	**-3.245**	**	0.359	0.996	1.052	0.826

6.4.4 Bumblebee forage plant use

All bumblebee foraging visits observed during this study were made to a total of nine different plant species (table 6.8). More than half of these visits were to one species, *T. pratense* and over 85% of all foraging visits were made to just three species, *T. pratense*, *Prunella vulgaris* and *T. repens*. The most frequently visited species in June were *T. repens* and *Lotus corniculatus*, with *P. vulgaris* and *T. pratense* were the most commonly visited species in July and August, respectively.

Table 6.8: The total number of inflorescences of each forage plant species recorded throughout the survey period and the overall proportion of foraging visits made by bumblebees to each of these plant species

Species	**Total no. inflorescences**	**% Total bumblebees**
Trifolium repens	5582	12.19
Trifolium pratense	2686	57.95
Odontites verna	1457	4.23
Lotus corniculatus	1327	4.48
Prunella vulgaris	1135	15.42
Rhinanthus minor	416	0.75
Vicia sepium	192	0.25
Vicia cracca	143	1.24
Succisa pratensis	64	3.48

6.5 Discussion

6.5.1 The effect of restoration treatment on the abundance of bumblebees and their forage plants

This study examined the efficacy of five different restoration treatments in providing forage plant material for bumblebees on an area of degraded machair grassland in the Hebrides. Of the five restoration treatments examined, the two wildflower treatments supported the highest density of foraging bumblebees. This is perhaps to be expected given that these two treatments included species specifically sown to provide bumblebee forage plant material including a high proportion of *Trifolium* sp. which are particularly favoured by bumblebees as a source of protein-rich pollen (Goulson & Darvill 2004; Goulson *et al*. 2005; Goulson *et al.* 2008b; Hanley *et al.* 2008). Here, however, we are able to quantify the magnitude of the differences in bumblebee abundance within specifically created seed mixes versus readily available, less expensive options.

The low numbers of bumblebees in the last year of this study are likely to be due to a very dry spring in the west of Scotland, which resulted in a delay in vegetation growth across the wider landscape. However, despite this, the two wildflower treatments recovered well by August and, similarly to the previous years, they attracted the highest number of bumblebees relative to the other treatment types. The dry spring and consequent lack of spring flowers had clearly impacted on bumblebee populations since all species remained scarce throughout 2010.

The 'Bird & Bee' treatment is already implemented at a number of nature reserves in Scotland, hence its inclusion in this study. The treatment contained both *T. repens* and *T. pratense* which were two of the most commonly utilized forage plant species. However, the availability of these species was relatively low when compared with their availability in the two wildflower treatments and the number of foraging bumblebees observed was also low in comparison to the wildflower seed treatments. In addition, the *Phacelia* component of the 'Bird and Bee' mix is known to be well utilised by foraging bumblebees (Carreck *et al*. 1999) but, as an annual species, it did not persist long enough to be detected as a bumblebee forage plant within the scope of this study. It should be noted that inclusion of this species in seed mixes for use on machair is inappropriate since it is a non-native species; our study also shows that it has limited and short-term value to bees.

The fallow treatment was included because second year fallow was identified in a previous study as providing an important source of forage material, particularly for rare *Bombus* species, in the Outer Hebrides (Charman 2007; Redpath *et al*. 2010). It is also relatively cheap to implement and mimics a traditional crofting practice (Kent *et al.* 2003). However, the success of this method in restoring degraded sites and improving species diversity is very much dependant on the availability of suitable propagules (Coulson *et al.* 2001). The seed buried in the soil seed bank contributes significantly to the regeneration of grassland vegetation after soil disturbance (Kalamees & Zobel 2002) but the density of seed in calcareous grassland soils and machair soils is generally very low (Owen *et al.* 2001; Redpath *et al. unpublished data*). Owen *et al.* (2001) suggest that any regeneration of machair vegetation following soil disturbance would most likely be from vegetative reproduction and not from the seed bank. Whilst the use of fallows on machair may increase habitat heterogeneity, if the species of key importance to foraging bumblebees are not present in the seed bank (or in close enough proximity to colonise the fallows from vegetative propagules or from seed rain), then the species composition of fallows is unlikely to support bumblebee populations.

6.5.2 Machair management recommendations for conservation of bumblebees

The two wildflower mixes attracted bumblebees throughout the season because the species composition of the seed mixes created a continuous availability of key forage plants. Several bumblebee studies have noted that the availability of key plant species throughout the season is of greater importance than high plant species diversity and this is something which should be considered when creating seed mixes targeted at bumblebee conservation (Bäckman & Tiainen 2002; Mänd *et al.* 2002; Charman 2007). *Trifolium pratense* and *T. repens* were particularly important foraging resources during this study and both species are typical of machair grassland so would be ideally suited to seed mixes created for machair restoration projects (Roberts *et al*. 1959; Kent *et al*. 2003).

Not only do the wildflower treatments provide a continuous availability of key species but they have demonstrated longevity as they continue to provide bumblebee foraging habitat four years after their initial implementation. Although the most expensive treatments to implement (table 6.1), ‘Wildflower 1’ and ‘Wildflower 2’ not only attract significantly more bumblebees than the other treatment types but they do so year after year. In addition, these treatments continue to flourish floristically, which in turn provides a source of seed rain which can, and does, colonise adjacent machair land with the native wildflower species on which the rarer *Bombus* species rely (N. Redpath pers. obs.).

The rationale for creating two similar wildflower mixes, one with and one without a grass seed component, was that although the wildflower mix with grasses is cheaper to produce, the grasses may have begun to out-compete the wildflower component over time, therefore reducing its value as bumblebee foraging habitat . This study found that in the case of machair, there was no significant difference in the abundance of wildflower inflorescences available in the two wildflower treatments after a four year period. 'Wildflower 1' was utilised by foraging bumblebees to the same extent as 'Wildflower 2' but cost less than half the amount to implement and so within the context of this study, 'Wildflower 1' is the most suitable treatment for restoring machair habitats for bumblebees. However, the initial cost of the wildflower seed required to restore machair is relatively high when compared to the use of commercial seed mixes or the creation of fallows (table 6.1). In order to encourage the implementation of such seed mixes, they would need to become incorporated into suitable agri-environment schemes which subsidise the cost of the seed and include payments to ensure that the machair is suitably managed. Current agri-environment schemes in Scotland, which run 2007-2013, do not include bumblebee specific options but they do include a package of land management options designed to reinstate machair of high biodiversity value (Scottish Government 2010). One of the options in this package is entitled 'management of species-rich grassland' and farmers or crofters who implement this option on machair must sow species native to the local region and maintain the grassland through an appropriate grazing and/or cutting plan. Agri-environment payments for this option are paid at a rate of £111/ha per annum over a five year period, with an additional one off payment of £680/ha towards the capital cost involved in obtaining the necessary seed. Without further incentives, uptake of this option using the wildflower mixes described here is likely to prove prohibitively expensive given that the seed alone cost £1890 per ha.

However, it is not simply the implementation of species rich seed mixes which will safeguard the diversity of machair grasslands. A review of restoring species rich grassland in France highlighted the importance of active grassland management and the avoidance of abandonment in order to prevent the rapid growth of highly competitive species (Muller *et al*. 1998). Carvell (2002) looked at the effect of land management on bumblebee abundance on Salisbury Plain training ground (southern England), the largest area of unimproved chalk grassland in North West Europe. Her study demonstrated that grazing, preferably by cattle, created more suitable bumblebee foraging habitat than unmanaged grassland and that small scale disturbances from vehicles have a similar effect.

The existing ‘management of species-rich grassland’ agri-environment option is not targeted specifically at bumblebee conservation and therefore, there is no requirement to include specific bumblebee forage plant species. For rare bumblebees to be effectively conserved in areas where machair has become degraded wildflower seed mixes such as ‘Wildflower 1’, which contain key forage plant species, should be implemented in combination with an appropriate cutting and grazing regime. This will encourage the persistence of wildflower species over a number of years and improve the availability bumblebee forage material throughout the season whilst allowing crofters, farmers and land managers to continue producing silage and grazing livestock.

The decline in bumblebee numbers across much of Western Europe has been well documented and considerable effort has been made in terms of establishing how best to manage habitat in intensively farmed agricultural landscapes for bumblebees (Kells *et al*. 2001; Bäckman & Tiainen 2002; Carreck & Williams 2002; Carvell *et al*. 2007; Osborne *et al*. 2008; Lye *et al*. 2009; Potts *et al*. 2009; Westphal *et al*. 2009). However, many key populations of rare *Bombus* species now exist only in pockets of habitat which have escaped widespread agricultural intensification and these areas are often subject to land management practices which differ from those commonly implemented in large scale farming systems.

In conclusion, this study highlights the efficacy of specific wildflower seed mixes in attracting foraging bumblebees, including rare species, to areas of formerly degraded machair. In addition, if seed mixes contain species typical of machair grassland plant communities, then areas of machair which have lost floral diversity due to relatively recent changes in land management practices can be restored in such a way that they are able to continue supporting populations of rare *Bombus* species. Some of the most effective methods for restoring intensively managed grassland elsewhere in the UK have proved to be extremely time consuming; for example, nutrient stripping, de-turfing and reseeding (Pywell *et al*. 2007). This research demonstrates that efforts to restore bumblebee forage plants to machair could be a more straight forward process involving ploughing and reseeding, practices which do not require specialist equipment other than agricultural machinery already available to most crofting communities in the west of Scotland (Osgathorpe *et al*. *unpublished data*). Unlike the agricultural intensification which has swept across much of Western Europe since the Second World War, degradation of machair is relatively recent and this study demonstrates that it is possible to restore wildflower-rich machair habitat relatively rapidly when suitable re-seeding and grazing regimes are implemented.

7 General Discussion

The primary objective of this thesis was to explore and develop strategies for managing florally-rich machair grassland habitats in order to deliver foraging resources for rare bumblebees. Machair habitats have become fundamentally linked with, and indeed are maintained by, the crofting practices which take place on and around them (Roberts *et al*. 1959; Angus 2001; Ward & MacKintosh 2001; Kent *et al.* 2003; Love 2003).The word “croft” means a small area of enclosed land (The Oxford Modern English Dictionary 1995) but unfortunately it is the small-scale nature of crofting which has rendered the practice economically unviable in the current competitive agricultural market (Willis 1991). Consequently, traditional machair cropping practices have largely been replaced by intensified grazing regimes, silage production or the abandonment of agricultural practices altogether, which has in turn resulted in machair that is low in plant species diversity (Kent *et al*. 2003).

Species-rich machair has become a stronghold for a number of rare and declining species including *Bombus distinguendus*, the UK’s rarest bumblebee (Goulson 2003a; Benton 2006). Therefore the degradation of this unique habitat has severe implications for the continued survival of *B. distinguendus* populations in the UK. In order to develop methods for restoring foraging resources for bumblebees on degraded machair, I looked first at how bumblebees utilise machair habitats in Western Scotland and more specifically I examined the foraging behaviour of the UK’s rarest *Bombus* species, *Bombus distinguendus* (chapter 2). Secondly, I presented an overview of how current land management practices implemented in the crofted regions of North West Scotland, affect the abundance of bumblebees and their foraging resources (chapter 3). One of the land management practices observed on crofts in these regions was the implementation of an agri-environment scheme designed to provide early cover habitat for corncrakes. It has been proposed that the habitat requirements of corncrakes and bumblebees overlap to some extent (Benton 2006) and so I examined the efficacy of existing early cover plots in attracting foraging bumblebees across the island of North Uist in the Outer Hebrides (chapter 4). Finally, I established the potential for restoring florally-rich machair habitats from the existing machair seed bank and considered the results of a four year field trial, which compared the attractiveness of five machair restoration treatments to foraging bumblebees (chapters 5 and 6). The following general discussion summarises the findings of this work, describes the limitations of these findings and draws conclusions as to how they may be applied to future bumblebee conservation strategies implemented on machair habitats.

7.1 Summary of work

During this research, the most frequently observed bumblebee species on machair were *B. muscorum* and *B. distinguendus*, both of which are UK Biodiversity Action Plan priority species. It has been suggested that the rarer, later emerging species such as these are largely associated with open semi-natural grassland habitats because these habitats lack the early flowering plant species which support earlier emerging *Bombus* species, thus competition for resources is reduced (Williams 2005). Overall, of the 25 *Bombus* species native to the UK, only five species were found foraging on the machair grasslands of the Outer Hebrides. This figure is much lower than the number of species observed foraging on semi-natural grasslands elsewhere in the UK and Europe (Carvell 2002; Mänd *et al*. 2002; Goulson & Darvill 2004; Öckinger & Smith 2007; Goulson *et al*. 2008).

In addition to the records of foraging *B.distinguendus* collected on machair during this study, existing records of *B. distinguendus* from across its Scottish range have been compiled in order to present an overview of how this species uses different forage plant families. This revealed that the greatest proportion of *B.distinguendus* foraging visits (Scottish range only) were to plant species from the Fabaceae, Rosaceae and Scrophulariaceae families. Interestingly, observations of *B. distinguendus* collected on machair highlighted the importance of *Centaurea nigra* and the preference indices calculated suggested a strong preference for *Cirsium vulgare*, both of which are Asteraceae species. However, records from across the species wider Scottish range have consistently demonstrated that the most commonly utilized forage plants belong to the Fabaceae family and *T. pratense*, which is widely recognised as a key forage plant for many bumblebee species, is particularly frequently visited (Bäckman & Tiainen 2002; Mänd *et al*. 2002; Goulson & Darvill 2004; Goulson *et al*. 2005; Diekötter *et al*. 2006; Goulson *et al*. 2006; Charman, 2007; Goulson *et al*. 2008a; Goulson *et al* 2008b).

The highly intensive nature of farming in Western Europe is considered to be the primary factor driving bumblebee declines (Goulson 2003; Benton 2006; Goulson *et al*. 2008a). However, the data presented in chapter 3 demonstrate that even in the crofting systems of North West Scotland, which have only been subjected to intensified agriculture relatively recently, bumblebees and their forage plants are present only at very low densities. Of particular concern is the fact that *B. distinguendus* was only observed twice during surveys on crofted land, even though the wider study area is believed to encompass some of the few remaining strongholds for this species in the UK (Benton, 2006; Goulson, 2003a).

The different land management practices undertaken on crofts, varied throughout the season in their attractiveness to foraging bumblebees, reiterating the importance of a heterogeneous agricultural landscape in order to provide a succession of forage material (Weibull *et al*. 2003). Although some land management practices were identified as being more beneficial than others in terms of promoting forage plant availability and bumblebee abundance, the low overall number of bumblebees recorded on crofts suggests that none of the management types surveyed are of significant benefit to the conservation of bumblebees. In particular, this study has demonstrated that there is a marked negative relationship between the abundance of foraging bumblebees and habitats grazed by sheep. Pasture that had been sheep grazed, even for a short period of time, supported a negligible number of bumblebees and therefore, management of sheep is a key factor in determining the value of crofts for bumblebees.

In addition to *B. distinguendus*, machair grasslands and crofting systems in general are associated with another species which has declined significantly as a result of agricultural intensification, the corncrake (*Crex crex*) (Green & Stowe 1993). Parallels are often drawn between *C. crex* and *B.distinguendus* as both species have undeniably declined as a result of changes in grassland management. However, specific habitat creation and management for *C. crex* in the Outer Hebrides was not found to be of significant benefit to *B. distinguendus* and the numbers of foraging bumblebees observed in early cover habitat patches were consistently low.

Not only did this research examine the foraging behaviour of bumblebees in existing habitats, but chapters 5 and 6 looked more specifically at potential methods for reinstating floral resources to areas of degraded machair. The machair seed bank, sampled at several locations in the Outer Hebrides, was found to have a much greater seed density than previously thought. The mean density of the machair seed bank data presented here (908 seeds m^{-2}), although still low relative to the seed banks of many other habitats, was found to be more than 15 times the maximum density previously calculated for machair sites in South Uist (58 seeds m^{-2}; Owen *et al*. 2001).

Despite this new evidence, which suggested that the soil seed bank of machair grassland is denser than previously thought (Owen *et al*. 2001), some plant species which are characteristic of machair vegetation (Kent *et al*. 2003) were not found in the seed bank during this study. These included *C. nigra* and *T. pratense,* both of which have been described above as key bumblebee forage plants. These species, in conjunction with a small number of other native wildflowers, form a suite of forage plants which are utilised by *B. distinguendus* and it is their availability within machair grasslands which is likely to have resulted in the strong association between the habitat and this rare *Bombus* species (Charman 2007; Redpath *et al*. 2010). The absence of these species in the seed bank corroborates the need for field trials such as the one described in chapter 6 of this thesis, which examines five different machair restoration treatments. The restoration treatments included seed mixes, which will ultimately be required to restore bumblebee forage plants to machair habitats if key species are absent from the existing vegetation or seed bank.

Of the five restoration treatments examined here, the two wildflower-rich seed mixes supported the highest abundance of foraging bumblebees but given that these two treatments included species specifically sown to provide bumblebee forage plant material, this is perhaps unsurprising. The 'Bird & Bee' seed mix which was trialled, is currently implemented at a number of nature reserves in Scotland and in some of the early cover plots described in chapter 4. However, the availability of key forage plant species was relatively low in this mix when compared with their availability in the two wildflower treatments and hence few foraging bumblebees were observed on this treatment. These mixes, which were originally designed to provide seed for over wintering passerines, but which have now been enhanced with plant species aimed at attracting bumblebees (Bridge 2007; Beaumont & Housden 2009), consist largely of non-native components such as *Phacelia tanacetifolia.* Although undoubtedly rewarding for bumblebees (Walther-Hellwig & Frankl 2000; Westphal *et al.* 2006), these mixes could be considered inappropriate for implementation in agricultural systems which encompass rare, species-rich habitats such as the machair.

Some of the treatment plots on Oronsay were left to go fallow and regenerate naturally from either the seed bank or seed rain. The success of this method in restoring degraded sites and improving species diversity is very much dependant on the availability of suitable propagules (Coulson *et al.* 2001). Whilst the implementation of fallow areas on machair may be relatively cheap, if the key forage plant species are not present in the seed bank as is suggested by the data collected in chapter 5 of this thesis, then the species composition of fallow areas cannot be guaranteed to support foraging bumblebees on machair habitats.

7.2 Implications for future machair management

The diversification and restoration of grassland habitats frequently requires the introduction of species in the form of specific seed mixes (Coulson *et al*. 2001) and the research presented here suggests that machair is no exception. Some species have a more persistent seed bank than others and therefore, restoration of grassland habitats from the existing seed bank can result in a disproportionately high representation of non-target species in the emergent vegetation (Bakker & Berendse 1999).

In order to achieve a specific outcome, which in the case of this research is an abundance of bumblebee forage plant species, the introduction of specifically designed seed mixes is often the most realistic restoration strategy. However, of the seed mixes trialled here, the most successful at delivering foraging resources for bumblebees were also considerably more expensive to implement than the alternative options. The sowing rate of these seed mixes could potentially be reduced in order to lower the cost of implementation, but it would inevitably take a longer period of time to create the desired end point of wildflower-rich habitat (Coulson *et al.* 2001). One option, suggested by Pywell *et al.* (2007) who also found the most expensive grassland restoration option to be the most effective, is to create small focal areas utilizing the most expensive but effective method and thus these areas can act as the source of seed from which neighbouring areas of land can be colonised. This method could potentially enhance the availability of important, target forage plant species by improving their availability in the seed rain. Although further research would be required in order to substantiate this proposal, the observed dispersal of seed from treatment plots to non-target areas during the restoration trial on Oronsay (chapter 6) would suggest that this strategy could be a distinct possibility for enhancing bumblebee forage plant availability on machair habitats, thus mitigating the need to implement vast areas of these species in the form of expensive seed mixes.

The ability of seed to move between sites is also important if a species is to become widely distributed across a landscape. Therefore, the implementation of dispersed patches of bumblebee forage plant species should be supplemented with appropriate seed dispersal strategies. Grazing regimes undoubtedly have an impact on the abundance and diversity of species within grassland habitats and the movement of livestock between sites is likely to be advantageous with regard to the dispersal of seed (Bakker & Berendse 1999; Coulson *et al*. 2001). The production and movement of hay between sites may also have a similar effect although the cutting date of grass crops has a significant affect on the efficacy of this strategy (Coulson *et al*. 2001). Many grassland species produce seed which do not ripen until June at the earliest and this has significant implications for grassland which is harvested for silage as early as May, before wildflowers have had the opportunity to set seed (N. Redpath pers. obs.). Coulson *et al.* (2001) highlight the fact that although some species can reproduce vegetatively, this only maintains the presence of a species within a localised area and so for a species to proliferate widely it must set seed.

It is worth noting that the uptake of the corncrake early cover agri-environment scheme, outlined in chapter 4, was relatively high, at least in part because it involved participants sacrificing only a small proportion of their croft to the scheme. With this principle in mind, it is possible that the process of implementing relatively small patches of high quality bumblebee forage plants across numerous crofts within *B. distinguendus'* current range could be a more realistic bumblebee conservation option than attempting to reinstate larger areas of species-rich habitat. Studies which have assessed the possibility of improving habitats for the purpose of enhancing biodiversity, clearly state that for a habitat management strategy to be effective, region specific influences must be taken into account (Williams & Osborne 2009). In the case of conserving *B. distinguendus* within its current UK range, these region specific influences involve incorporating agri-environment schemes into the crofting system. As crofts themselves are relatively small units of land, it is conceivable that agri-environment schemes designed to influence a relatively small proportion of land will be more favourable to potential agri-environment participants.

This body of work highlights the efficacy of specific wildflower seed mixes in attracting foraging bumblebees, including rare species, to areas of formerly degraded machair. If seed mixes containing species that are typical of machair grassland plant communities are distributed across areas of machair which have lost floral diversity due to changes in land management, then it is possible that they will have the potential to restore foraging resources for populations of rare *Bombus* species. However, these findings would need to be incorporated into agri-environment schemes which are available and applicable to, the crofted regions of North and West Scotland.

7.3 Conclusions and bumblebee conservation recommendations

There are undoubtedly a number of issues contributing to the decline of bumblebees but a lack of suitable foraging resources, as a result of intensified agriculture, is likely to be the most influential of these factors (Goulson 2003a; Edwards & Williams 2004). The results presented here support the findings of several authors which document that the foraging requirements of the rarer species such as *B. distinguendus*, do not involve complex specialisations, but instead they require a successional availability of relatively common native wildflowers (Goulson *et al*. 2006; Charman 2007).

Finally, whilst declines in *B. distinguendus* are now well recognised, there is some anecdotal evidence to suggest that the species is expanding its geographic distribution in Scotland. It is unclear whether this is a genuine range expansion or perhaps more likely, a heightened awareness of the species and consequently an increased surveying effort has captured a truer representation of the species' current UK distribution (Bumblebee Conservation Trust 2010). However, if this recent range expansion is to be maintained or even expanded further, there is a genuine need for the implementation of agri-environment schemes targeted specifically at bumblebees within the fragmented agricultural landscapes of northwest Scotland and I propose the following key recommendations for future schemes:

- **In order to enhance existing habitat for *B. distinguendus*, future agri-environment schemes should promote the implementation of pollen and nectar rich seed mixes that include native species from the Fabaceae and Asteraceae families and in particular, *Trifolium repens*, *Trifolium pratense* and *Centurea nigra*.**

- **These schemes should be specifically targeted at the agricultural systems that now support remaining fragmented *Bombus* populations, such as the crofting systems of northwest Scotland, as the successful conservation of our most endangered *Bombus* species will rely on the provision of suitable foraging resources throughout its current range.**

- **Once pollen and nectar seed mixes have been implemented in suitable locations, they must be actively managed by cutting and/or grazing annually in the autumn/winter, once plant species have set seed.**

- **The use of artificial fertilisers, herbicides and pesticides should be prohibited on land where pollen and nectar mixes are implemented**.

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