

**Reconciling ecology and economics to conserve
bumblebees**

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Abstract

Many bumblebee species have experienced severe population declines in response to the use of intensive land management practices throughout the UK and western Europe during the latter half of the twentieth century. The loss of wildflower-rich unimproved lowland grasslands has been particularly detrimental and, as a result, in the UK two bumblebee species are now extinct, seven are listed on the UK Biodiversity Action Plan (BAP), and only six extant species remain common and ubiquitous. Populations of the rarer species are often fragmented and restricted to isolated areas, such as the crofting regions of northwest Scotland, in which the use of intensive farming practices has remained relatively limited. Consequently, in this study I primarily focus on the conservation of *B. distinguendus* and *B. muscorum*, two of the UK's rarest species which have strongholds in the Outer Hebrides. In this region crofting is the dominant form of agriculture, and is traditionally typified by small-scale mixed livestock production accompanied by rotational cropping activities. With the use of very few artificial inputs, traditional crofting activities are environmentally sensitive and promote the diverse wildflower assemblages characteristic of the machair which provide suitable forage for bumblebees. However, the changing demographic structure of the islands, in conjunction with a range of other socio-economic factors, is resulting in the adoption of more intensive land management practices by crofters and changing the nature of the crofted landscape. These changes are likely to have a detrimental impact on the rare bumblebee populations that rely on crofting to provide suitable foraging habitats. Neglecting to examine the socio-economic issues behind the decline in crofting activities, and failure to develop a means of making the system economically viable and sustainable, is likely to reduce the effectiveness of any bumblebee conservation measures introduced in the region. Through my research I address this socio-ecological problem by taking an interdisciplinary approach, and combine the two disciplines of ecology and economics to find a way to ensure crofting is

sustainable whilst promoting sympathetic land management practices to aid bumblebee conservation. The results of my research demonstrate that current croft land management practices do not support high abundances of foraging bumblebees in the Outer Hebrides, and that sheep grazing during the summer has a particularly negative impact on bumblebee abundance on croft land. My research also highlights the importance of non-agricultural habitats for foraging long-tongued bumblebee species in agricultural landscapes. Grazing management can promote bumblebee abundance, with cattle grazing providing a valuable foraging habitat for short-tongued bumblebees in southwest England. Therefore, to conserve bumblebees in agricultural landscapes the type of farming system needs to be taken into account in developing grazing management regimes, whilst non-agricultural habitats need to be integrated into local land management plans to ensure the provision of forage for bumblebees throughout the flight period. The outputs of the ecological-economic models show that compensation payments are not always required to encourage beneficial land management practices to enhance bumblebee populations in crofted areas. However, crofting is a marginal farming system that is heavily influenced by socio-economic factors, and this should be taken into consideration in the development of future agricultural policy for the region.

Declaration

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

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Lynne M. Osgathorpe

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Chapter 1. Introduction

1.1. Background

Agriculture is the predominant land-use type in the EU (Robinson and Sutherland, 2002), accounting for over 45% (>189 million ha) of the total land mass of the EU-27 nations (FAO, 2010), and more than 77% of the total UK land mass (DEFRA, 2007). In the EU, the Common Agricultural Policy (CAP) is the primary legislation governing farming, and has been the principal driver of agricultural change throughout northwest Europe since its inception in the mid-twentieth century. Due to the close relationship between farm practices and farmland biodiversity, the mechanisation and intensification of agriculture resulting from the CAP inevitably had a negative impact on the persistence of many farmland species throughout Europe. The loss of many traditional farming practices was particularly detrimental as it resulted in a widespread reduction in landscape heterogeneity and the subsequent loss of many semi-natural habitats from agricultural areas (Chamberlain *et al.*, 2000; Robinson and Sutherland, 2002; Henle *et al.*, 2008). Bumblebees (*Bombus* spp.) are one of many taxonomic groups that have suffered population declines throughout northwest Europe in response to changing farming practices (Goulson *et al.*, 2008a). In the UK, seven species are listed on the Biodiversity Action Plan (BAP) as threatened and in need of conservation, whilst two species went extinct in the last century (Benton, 2006). The decline of these important pollinators and other species associated with farmland habitats has now been recognised and, following several reforms, the CAP has refocused its aims away from maximising crop yields to include the conservation of farmland biodiversity.

1.2. Agricultural policy throughout the twentieth century and its impacts on farmland biodiversity

1.2.1. Agricultural policy in the twentieth century

By the early twentieth century much of the UK's arable land had been abandoned or converted to pastoral use following the removal of government support during the mid-nineteenth century (Robinson and Sutherland, 2002). The availability of cheap imports from the US kept arable production at a minimum, and by 1940 two thirds of the UK's food was imported (Lloyd and Wibberley, 1977). Limited farm production and the unreliability of imports throughout the Second World War and early post-war period frequently led to food shortages and highlighted the need to create a self-sufficient farming industry where food supplies were guaranteed (Robinson and Sutherland, 2002). Consequently, the Agriculture Act was passed in the UK in 1947 (Robinson and Sutherland, 2002). The Act actively encouraged investment in British farming through capital grants, subsidies and sustained crop prices, and resulted in an increase in the area of arable land (Robinson and Sutherland, 2002). The injection of capital into farming during this period, coupled with the removal of restrictions to ploughing old grasslands in 1939, kick-started the British farming industry and signalled the beginning of agricultural intensification in the UK (Duffey *et al.*, 1974; Robinson and Sutherland, 2002; Hodgson *et al.*, 2005).

In line with the UK, many other western European countries faced these same food production issues, and this formed the driving force behind the creation of the CAP. Developed in the early 1950s, the aim of the policy was to create a self-sufficient economic community in which member states were guaranteed a reliable food source and a viable agricultural industry (European Commission, 2009). Financial aid in the form of production linked subsidies were introduced to ensure farmers received high prices for

their goods and to encourage them to produce greater yields. This was supported by initiatives created to increase the efficacy of farming practices through technological developments and the simplification of agricultural processes (Stoate *et al.*, 2001; European Commission, 2009). Consequently, many of the impacts of agricultural intensification experienced in the UK were also experienced throughout much of western Europe (Stoate *et al.*, 2001).

A range of economic factors, in addition to the incentives available under the CAP, helped stimulate agricultural intensification across the EU during this period. The increasing opportunity costs associated with hired labour (*i.e.* the cost of foregoing an alternative labour use) relative to other agricultural inputs led to farmers favouring new, more intensive methods that increased production per unit of labour (Hayami and Ruttan, 1985), therefore driving the mechanisation of many farming activities (Strijker, 2005). In addition, the low market price of inorganic fertilizers led to an increase in fertilizer use (Strijker, 2005), with applications to permanent grasslands in England and Wales rising from 37% of grasslands in 1962 to 77% in 1982 (Wells and Sheail, 1988), and from 20 kg ha⁻¹ to 90 kg ha⁻¹ (Hodgson *et al.*, 2005). The high price of cereals, particularly during the 1970s, continued to drive intensive farming practices, with the drainage of low-lying wetlands and the conversion of grasslands to arable production occurring throughout the EU (Stoate *et al.*, 2001; Hodgson *et al.*, 2005). The CAP was particularly successful in encouraging farmers to maximise their yields; however, by the 1980s production had outstripped demand and agricultural surpluses of 20-30% were being recorded (Robinson and Sutherland, 2002). In addition, by this period the negative impacts of modern agricultural practices on farmland biodiversity were also being recognised. In order to address the environmental impacts of farming the CAP started to refocus its aims onto the provision of environmental services. This began with the introduction of Environmentally

Sensitive Areas (ESA), a flat-rate payment scheme designed to encourage farmers to utilise environmentally sensitive practices (Hodgson *et al.*, 2005). Since then, European agricultural policy has continued to develop with a more environmental focus. In 1992 the MacSharry CAP Reform addressed the issues of overproduction and set out requirements for member states to develop Agri-Environment Schemes (AES) (Stoate *et al.*, 2001; European Commission, 2009), whilst further reforms took place in 1999 and 2003 (European Commission, 2009). The former, known as ‘Agenda 2000’ aimed to give the EU a new financial framework to strengthen and prepare the union for enlargement in 2004 (European Commission, 1999). Policies relating to agriculture and the environment echoed those introduced in previous reforms (European Commission, 1999), and introduced rural development policies to aid the development of rural communities and help farmers diversify their activities and maintain viable businesses (European Commission, 2009). Key changes to agricultural policy were introduced through the most recent (2003) CAP reform, most notably the decoupling of production linked subsidy payments. With effect from 2005, farmers received payments independent of output through the Single Payment Scheme (SPS), and more emphasis was placed on conserving the environment through AES (European Commission, 2009). As a result of these reforms, today’s CAP retains an environmental focus where farmers and land managers are compensated for implementing environmentally sensitive management practices, diversification of farm businesses is encouraged, and support is provided to aid the development of rural communities.

1.2.2. Agricultural intensification and biodiversity

The effects of intensification are far reaching, from modifying the farmed environment at the landscape scale to driving population declines in a wide variety of farmland species (Chamberlain *et al.*, 2000; Robinson and Sutherland, 2002; Berendse *et al.*, 2004). At the

landscape level, technological advancements resulted in the simplification of farming systems and the subsequent homogenisation of the agricultural landscape (Stoate *et al.*, 2001). Throughout the UK and western Europe the number of farms declined whilst overall farm sizes increased and non-cropped habitats were removed (Stoate *et al.*, 2001; Robinson and Sutherland, 2002). The rapid loss of important landscape features such as hedgerows was driven by the availability of capital grants under the CAP, whilst grasslands were irrigated to increase the area of productive arable land. The effect of agricultural intensification on grassland habitats throughout the UK is particularly staggering, with 90% of unimproved lowland grassland lost between 1932 and 1984 (Fuller, 1987), and 80% of calcareous grassland lost or damaged between 1949 and 1984 (Newbold, 1989). As well as the loss of non-crop habitats, the simplification of farming practices led to farming becoming increasingly specialised and geographically separated. Farmers in the west of the UK predominantly focused on livestock production whilst farmers in the east of the country favoured more intensive, large scale arable systems.

Habitat loss and fragmentation arising from the use of intensive practices resulted in extensive declines of many species associated with agricultural landscapes (Chamberlain *et al.*, 2000; Robinson and Sutherland, 2002), and these impacts are particularly noticeable in populations of farmland birds (*e.g.* Chamberlain *et al.*, 2000). For example, the shift from spring sown to winter sown crops led to a reduction in the availability of stubble for granivorous species such as corn bunting (*Miliaria calandra*) and linnet (*Carduelis cannabina*), both of which experienced severe populations declines between 1969 and 1995 (Chamberlain *et al.*, 2000). Many waders, including lapwing (*Vanellus vanellus*), also declined as a result of this more intensive practice. These birds often breed in spring sown fields where the emerging crops provide cover for nests and chicks; however, winter sown crop stands reach a much greater height during the breeding season therefore making

the land unsuitable for nesting and breeding. In addition, Birdlife International (2004) has shown that the current downward trends exhibited by many farmland bird populations are significantly correlated to cereal yields, providing a link between intensification and farmland bird populations.

The botanical composition of farmland can also be affected by the use of more intensive practices (Stoate *et al.*, 2001). Declines in many spring germinating arable plants such as the corn marigold (*Chrysanthemum segetum*) have been linked to changes in the timing of cultivation from spring to autumn (Stoate *et al.*, 2001; Robinson and Sutherland, 2002), whilst spray drift has led to changes in the botanical composition of plant communities in field margins (Stoate *et al.*, 2001). Similarly, the invertebrate communities associated with agricultural habitats are often negatively affected by changing practices (Robinson and Sutherland, 2002). The shift from hay to silage production, coupled with an increase in the use of artificial fertilizers enables faster growing grasses to outcompete wildflowers, whilst earlier cutting reduces seed set which decreases the diversity and abundance of wildflowers in the seed bank. Ultimately, this results in the loss of unimproved wildflower meadows and therefore key foraging habitats for invertebrates. For example, di Giulio *et al.* (2001) demonstrate that Heteropteran diversity is lower in more intensively managed meadows. Likewise, Kosior *et al.* (2007) found that the loss of landscape heterogeneity coupled with other aspects of intensification, such as increased pesticide use, had a negative impact on bumblebee populations in nine of the 11 western and central European countries examined within their study. The conservation of farmland biodiversity is now a key element of the CAP, with policies now focusing on encouraging farmers to utilise environmentally sensitive methods and restore farmland biodiversity.

1.3. British bumblebees: Ecology and conservation

1.3.1. An introduction to bumblebee ecology

Bumblebees are charismatic insects commonly recognised by their large size, dense covering of hair and distinctive markings (Plate 1.1). They are members of the Hymenoptera, an immensely diverse insect order that also includes wasps, sawflies and ants, and they belong to the sub-order Aculeata alongside other bee groups (Benton, 2006). Although at times hard to distinguish from other bees, bumblebees form a separate genus: *Bombus*, and exhibit a variety of colourations other than the black and yellow bands typically associated with this group (Plates 1.2 and 1.3). The evolution of dense hair across the thorax and abdomen provides bumblebees with a suitable adaptation to cooler climates, therefore most species are distributed throughout temperate regions of the northern hemisphere (Benton, 2006). However, some species are able to persist in warmer climates, with populations found in southeast Asia, and tropical and central America (Benton, 2006).

The life cycle of most bumblebee species tends to be completed on an annual basis, starting with the emergence of queens from hibernation in late winter and spring (Goulson, 2003a). After emergence, queens actively forage and begin searching for a suitable nesting site. Emergence times vary between individual species, as do the habitats and locations in which they choose to nest (Svensson *et al.*, 2000). Once a suitable nest site has been chosen the queen lays between 8-16 eggs in a wax covered pollen ball which she then incubates (Goulson, 2003a). After a period of approximately four days the larvae emerge and feed on the pollen ball. The queen continues to incubate the brood but must also continue foraging for both pollen and nectar, which renders this early stage of nest development one of the most critical (Schmid-Hempel, 1998). After 10-14 days when the first larvae are fully developed they pupate for another two weeks bringing development

time to approximately 4-5 weeks (Goulson, 2003a). The first offspring to emerge are usually workers (females) which are tasked with foraging, maintaining the nest and rearing subsequent broods. The emergence of workers allows the queen to remain in the nest and continue laying eggs, enabling the colony to grow rapidly in size (Goulson *et al.*, 2002). Once a critical nest size is reached, usually somewhere between April and August (depending on species), the queen switches from producing workers to males and queens (Goulson, 2003a). Generally, from this point onwards no further workers are produced. Bumblebees have an unusual genetic composition, known as haplodiploidy, that is characteristic of social Hymenoptera. Males are produced from unfertilised eggs and are therefore haploid, whilst females have a full diploid complement of chromosomes (Fournier, Aron and Milinkovitch, 2002). Consequently, the queen is able to control the sex of her offspring. Once the queen starts producing reproductives, workers may also produce eggs; as workers are unmated their offspring are also male. The new queens and males leave the nest to reproduce, with queens mating once and then going into hibernation ready to start the cycle again the following year (Baer and Schmid-Hempel, 2003). The bumblebees remaining in the founding nest often come into conflict with one another as workers attempt to lay eggs, and the nest quickly goes into decline and eventually dies (Baer and Schmid-Hempel, 2003; Goulson, 2003a).

The social life of bumblebees is particularly complex and has a eusocial structure. Eusociality is a cooperative behavioural trait characterised by three general properties: reproductive division of labour; overlap of generations; and cooperative brood care. As such, eusociality demonstrates an extreme form of altruism whereby the altruist (in this case the worker bumblebee) forgoes the ability to reproduce in favour of raising the offspring of one sexually reproducing individual (*i.e.* the queen; Benton and Foster, 1992; Danforth, 2002; Queller and Strassmann, 2003). Although eusociality appears to be

somewhat of an evolutionary paradox, Hamilton's theory on kin selection helps explain the evolution of this behavioural trait through natural selection, which he suggests will favour the development of altruistic behaviours when the relatedness of the altruist to the beneficiary is greater than the ratio of costs to benefits (Husseneder *et al.*, 1999; Roux and Korb, 2004). In terms of reproductive altruism, the trait will evolve in congregations of related individuals when either the relatedness between individuals is very high or the cost of altruism is low (Roux and Korb, 2004). The haplodiploid genetic composition of social Hymenopterans results in different degrees of relatedness between female offspring and their male siblings, and their potential offspring, which is thought to have facilitated the evolution of sociality in this group. Full sisters share 75% of their genes, whereas they only share 25% with their male siblings and 50% with their offspring. Consequently, by co-operating to rear the queen's offspring worker bumblebees are indirectly passing on their own genes whilst meeting a common interest in passing on their shared genes (Goulson, 2003a). However, this complex social structure has significant implications for conservationists assessing the status of bumblebee populations. Unlike many other organisms it is the *effective* population size rather than the total number of individuals that is required to measure the status of the bumblebee populations (Goulson *et al.*, 2008a). The effective population size is determined by the number of egg-laying queens and the number of males they have mated with (Goulson *et al.*, 2008a). However, because bumblebee colonies are founded by a single, typically monoandrous, queen and the males are haploid (*i.e.* develop from an unfertilised egg), the effective population size is only equivalent to 1.5 rather than two times the number of successful nests (Goulson *et al.*, 2008a). Consequently, it is the number of nests that provides an indication of population size, not the abundance of individual bumblebees, and for this reason it is likely that bumblebee populations exist at much lower densities than most invertebrates (Ellis *et al.*, 2006; Goulson *et al.*, 2008a).

In addition to the social bumblebees whose life history I have outlined above, there is a sub-genus of bumblebees known as the cuckoo bumblebees (sub-genus: *Psithyrus*). As the name suggests these species invade a bumblebee nest, usurping the queen and taking over her role as the only reproductive in the nest. Cuckoo bumblebees tend to emerge later in the season than other *Bombus* species and often parasitise a particular host species. For example, *B. vestalis* is a cuckoo of *B. terrestris*, whereas *B. rupestris* specialises in invading nests of *B. lapidarius*. Although they do not found their own nests the life cycle of cuckoo species is on an annual basis, and other aspects of their life history, such as mate location, are similar to other *Bombus* species (Goulson, 2003a).

Bumblebees rely on flowering plants as foraging resources and many species have formed strong associations with particular plants in which both organisms receive a mutual benefit: flowers provide nutritional rewards for the bumblebee whilst the insect aids plant reproduction (Proctor *et al.*, 1996). Bumblebee morphology plays a large part in these associations, as different species have different proboscis (or ‘tongue’) lengths (Benton, 2006). This enables bumblebees to exploit a range of different flowering species, with longer tongued species able to forage from flowers with deep corollas and short-tongued species visiting flowers with shallow corollas. Tongue length may therefore provide a simple means of grouping different species: *i.e.* ‘short’ (≤ 8 mm), ‘medium’ (8-9 mm) or ‘long’ (> 9 mm; Table 1.1; Goulson *et al.*, 2005). Interestingly, previous authors have found that species with longer tongues tend to be more specialised in their foraging preferences and are often rarer than species with shorter tongues (Goulson and Darvill, 2004; Goulson *et al.*, 2005; Goulson *et al.*, 2008a). This, and bumblebee habitat requirements are discussed in more detail in the following section.



Plate 1.1.

B. terrestris worker exhibiting the characteristic black, yellow and white striped markings often associated with bumblebees.

Source: L. Osgathorpe.



Plate 1.2. *B. muscorum* worker in the Outer Hebrides with a ginger thorax and yellow abdomen. Source: L. Osgathorpe.



Plate 1.3. *B. lapidarius* worker displaying a black thorax and abdomen, and red tail. Source: L. Osgathorpe.

1.3.2. *Bumblebees in the UK*

In the UK, 25 native species have been recorded (Benton, 2006); however, of these two (*B. cullumanus* and *B. subterraneus*) have gone extinct in the last 70 years¹ and a further seven extant species have experienced severe population declines (Benton, 2006). These are now formally recognised as endangered and are listed on the UK BAP (Table 1; Benton, 2006; Goulson *et al.*, 2008a). Only six bumblebee species remain common and ubiquitous throughout the UK (Benton, 2006). The effects of intensive farming have been particularly noticeable in bumblebee populations in the south, east and central areas of England where a reduction in the diversity and density of bumblebee species has created a ‘central

¹ A third species, *B. pomorum*, has not been recorded in the UK since 1864 (Benton, 2006).

impoverished area' where only the six most common species are frequently found (Williams, 1982; Williams and Osborne, 2009). In contrast, the rarest species are now confined to isolated areas that have not experienced the same levels of agricultural intensification as elsewhere in the UK (Goulson *et al.*, 2006). For example, *B. distinguendus* is restricted to crofted areas in northwest Scotland, and is often associated with the 'machair' habitats found along the north and west coasts of Scotland and western Ireland. Machair is a globally restricted and complex coastal habitat which is influenced by topography, shell content, grazing, climate and anthropogenic factors (Stewart, 1994). Typically, the term 'machair' refers to the low-lying grassland plain adjacent to the dune system (Stewart, 1994). Machair is formed from wind blown shell sand which produces a lime-rich soils (> pH 7.0), and creates a grassland habitat with several core plant species, including red clover (*Trifolium pratense*) and bird's foot trefoil (*Lotus corniculatus*; Stewart, 1994). which are important flowers for foraging bumblebees. In southern areas of the UK, fragmented populations of *B. sylvarum* survive on the lowland grasslands of Salisbury Plain, the Somerset and Gwent Levels, and Pembrokeshire (Benton, 2006). An explanation for the abundance of some species and decline of others has been put forward by Williams (1986, 1988), in the form of the 'marginal mosaic model'. This theory assumes that each species has its own optimum climatic range, in which species should be able to forage optimally, even in habitats which are not ideal. However, towards the edge of their climatic range bumblebees are assumed to only be successful in the most rewarding habitats, and present at lower abundances compared to the centre of the range. Consequently, should habitat quality decline, extinctions would be experienced at the range edges first, with species then retreating to the centre of their range. This concept appears applicable to some species, such as *B. distinguendus*, which is at the southern edge of its climatic range in the UK and has retracted northwards in response to habitat loss. However, the 'marginal mosaic model' does not provide satisfactory explanations for all

bumblebee declines, with some species undergoing declines even at the heart of their climatic ranges (Goulson, 2003a).

The loss of key floral resources from farmland habitats has made a significant contribution to bumblebee declines (Goulson *et al.*, 2008a). However, competition from introduced species (Goulson, 2003b), and the potential for pathogen spillover from commercially reared colonies (Colla *et al.*, 2006), have also been identified as possible drivers of this decline. Bumblebees are often associated with flower-rich unimproved grasslands (Williams and Osborne, 2009); however, during the last century much of this habitat was brought into production and many traditional practices, such as hay production and the use of red clover leys, were superseded by more intensive methods (Stoate *et al.*, 2001; Goulson *et al.*, 2008a). Consequently, the abundance and diversity of wildflowers declined, with preferred bumblebee forage plant species showing disproportionately greater reductions relative to other species (Carvell *et al.*, 2006; Goulson *et al.*, 2008a). The repercussions of habitat loss and the subsequent reduction in floral resources have generally been greatest for long-tongued bumblebees (*e.g.* *B. distinguendus*, *B. humilis*) which often specialise in collecting pollen and nectar from flowers with long corollas, particularly members of the Fabaceae (Goulson *et al.*, 2005). These plant species are often associated with semi-natural habitats that are now scarce in the agricultural landscape and, as a result, the bumblebees that exhibit the strongest associations with this plant family are all rare species (Goulson *et al.*, 2005). Conversely, short-tongued bumblebees are more general in their dietary requirements and exploit a wider range of floral resources (Goulson and Darvill, 2004; Goulson *et al.*, 2005), including non-native and cultivated flowers found in urban areas (Goulson *et al.*, 2002). This more generalised foraging behaviour exhibited by short-tongued bumblebees may help explain their more widespread distribution and abundance relative to the rarer long-tongued species.

Bumblebees require sources of forage throughout the flight period, therefore the spatio-temporal availability of floral resources within the landscape is essential for maintaining diverse bumblebee assemblages (Bäckman and Tiainen, 2002; Westphal *et al.*, 2006; Goulson *et al.*, 2008b). However, a mosaic of habitats is also required to provide bumblebees with suitable nesting sites (Goulson, 2003a; Goulson *et al.*, 2008a). Nesting requirements vary between individual species, with some exhibiting preferences for subterranean nest sites, such as banks (*e.g. B. terrestris*, *B. lucorum*), whilst others prefer tussocky vegetation (*e.g. B. pascuorum*; Goulson, 2003a). Nests are often located along uncultivated field boundaries (Banaszak, 1983; von Hagen, 1994); however, the widespread removal of hedgerows and loss of semi-natural grasslands is likely to have led to a reduction in the availability of these habitats (Goulson, 2003a; Goulson *et al.*, 2008a). In addition, more intensive production methods often lead to the destruction of above ground nests, whilst the loss of arable weeds from crop stands reduces the availability of forage for small mammals, whose abandoned nests are frequently utilised by nesting bumblebees (Goulson *et al.*, 2008a). The provision of hibernation sites within the landscape is also important (Goulson *et al.*, 2008a). The habitat requirements for hibernation sites are less well known, although the available evidence suggests that northwest facing slopes or shaded sites are preferred (Goulson, 2003a). However, it is likely that agricultural intensification has also reduced the availability of these habitats.

Table 1.1. The conservation status of bumblebee species in the UK. BAP species are highlighted in bold. Based on Benton (2006).

	<i>Species</i>	<i>Conservation status in the UK</i>	<i>Tongue Length</i>
<i>True bumblebees</i>	<i>B. lucorum</i>	Common and ubiquitous, stable	Short
	<i>B. terrestris</i>	Common and ubiquitous; northward extension of range	Short
	<i>B. soroeensis</i>	Widespread; local & declining in the south, more common in Scotland	Medium
	<i>B. cullumanus</i>	Extinct	Short
	<i>B. jonellus</i>	Widespread; local in the south, more common in Scotland	Short
	<i>B. pratorum</i>	Common and ubiquitous, stable	Short
	<i>B. monticola</i>	Widespread; local & declining in the northern and western upland areas	Short
	<i>B. hypnorum</i>	Recent colonist in UK	Short
	<i>B. hortorum</i>	Common and ubiquitous, possibly declining	Long
	<i>B. ruderatus</i>	UK BAP spp. Widespread; local in the southeast & east midlands	Long
	<i>B. lapidarius</i>	Widespread; local in the north; northward extension of range	Short
	<i>B. ruderarius</i>	UK BAP spp. Southern and local, declining	Long
	<i>B. pascuorum</i>	Common and ubiquitous, stable	Long
	<i>B. humilis</i>	UK BAP spp. Southern and local	Long
	<i>B. muscorum</i>	UK BAP spp. Widespread but local; mainly in coastal areas, declining	Long
	<i>B. sylvarum</i>	UK BAP spp. Rare; southern, very local, declining	Long
<i>B. distinguendus</i>	UK BAP spp. Rare; northern, very local, declining	Long	
<i>B. subterraneus</i>	UK BAP spp. Extinct, currently undergoing reintroduction at Dungeness	Long	
	<i>B. pomorum</i>	Extinct	Long
<i>Cuckoo bumblebees</i> (Subgenus: <i>Psithyrus</i>)	<i>B. vestalis</i>	Common and ubiquitous; more local in north & west	Short
	<i>B. bohemicus</i>	Common and ubiquitous	Short
	<i>B. rupestris</i>	Southern, increasing in some areas following population declines	Medium
	<i>B. barbutellus</i>	Common and ubiquitous, more common in south	Short
	<i>B. campestris</i>	Common and ubiquitous, stable	Short
	<i>B. sylvestris</i>	Common and ubiquitous, stable	Short

1.4. Crofting

1.4.1. The origins of crofting in Scotland

Crofting is an agriculturally based way of life that evolved following the Highland Clearances that took place throughout northern Scotland during the eighteenth and nineteenth centuries (Willis, 1991; Stewart, 2005). Consequently, crofting only exists in certain parts of Scotland known as the ‘Crofting Counties’, which 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). Prior to the Clearances, agriculture in the Highlands was predominantly based on self-sufficiency, with very few commercial commodities produced (Willis, 1991). Landlords therefore received their rents in grain, although poor harvests frequently meant that rents were not met (Willis, 1991). In contrast, demand for wool from the south (Hunter, 1991), and the willingness of sheep farmers from southern Scotland and northern England to pay rent for grazing livestock in the hills meant that sheep farming was a more reliable and profitable enterprise than traditional agriculture (Willis, 1991). Consequently, hundreds of rural communities were relocated to coastal areas by wealthy landowners in favour of intensive sheep farming (Willis, 1991; McIntosh *et al.*, 1994; Stewart, 2005). This ‘clearance’ of the Highlands was met with much resistance as Highlanders felt they had an historical collective right to the land, referred to as *dùthchas* in Gaelic (Willis, 2001; MacKenzie *et al.*, 2004). However, this claim was not recognised by the law and the rural population was relocated from their inland homes to coastal areas despite their resistance (Willis, 2001).

On the coast people were allocated small areas of land called ‘crofts’, derived from the Gaelic term *croit* (meaning small enclosed area of land; Stewart 2005), on which they could farm. Crofts were clustered together forming linear settlement patterns, known as

‘townships’, in which crofters implemented small scale rotational cropping regimes alongside livestock production (Stewart, 2005). However, land allocations were kept small by the ruling landlords to preclude crofters from total self-sufficiency, and were often located on unproductive land, which ensured that an additional source of income was always required by crofters (Stewart, 2005). By preventing self-sufficiency, landlords ensured that they had access to a cheap workforce to meet the large labour demands of the booming kelp industry, where workers were required to collect seaweed to be processed for use in the manufacture of soap and glass products (Hunter, 1991; Willis, 1991; Stewart, 2005). Kelp was an abundant natural resource in the Outer Hebrides, particularly on the Uists, therefore many families displaced through the Highland Clearances relocated from the mainland to these islands during the late eighteenth century (Caird, 1979). However, in response to the high demand for kelp, landlords encouraged larger families in order to supply their workforce and the population of the Crofting Counties increased dramatically in the early nineteenth Century (Willis, 2001). As a result, crofts were subdivided to provide land for additional families, food shortages were common and the land was overpopulated (Willis, 2001). The problems associated with overpopulation were exacerbated during the 1820s following the collapse of the kelp industry (Willis, 2001), and were compounded by the failure of the potato crop during the early 1840s (Willis, 2001). This culminated in the potato famine of 1846 (Willis, 2001; Stewart, 2005), which drove a mass emigration from the Crofting Counties (Stewart, 2005), with c. 60,000 people leaving for America, Canada and Australia between 1846 – 1861 (Cameron, 1986). As conditions continued to decline, animosity between crofting communities and the authorities developed during the latter period of the nineteenth century and led to the creation of a Royal Commission (known as the Napier Commission) in 1883 to examine the circumstances of crofters in the Highlands and Islands (Willis, 2001). Two years after the publication of the Napier Commission’s report, the Crofters’ Holding Bill was passed

through Parliament in 1886 and formed the first statutory guidelines for the organisation of crofting. The Bill safeguarded the rights of crofters, provided them with security of tenure, and created an incentive for crofters to improve the productivity of their land (Willis, 2001). Since 1886 there have been several further Commissions and Crofting Bills passed in Scotland, the Crofting Reform Bill (2007) being the most recent. Significant changes that have arisen from these crofting reforms include the legal right for crofters to buy their croft. Although 85% of crofters were still tenants to private landlords in 1990 (Crofters Commission, 1991), several communities have since bought-out their landlords, most notably in Assynt, and have therefore taken back their historic claims to the land.

1.4.2. Agricultural practices and the evolution of crofting during the twentieth century

The marginal nature of agricultural activities is a key aspect of crofting and has characterised the evolution of this agriculturally based social system (Willis, 1991; Stewart, 2005). Crofts are small agricultural units of enclosed land, typically on poor soils, and covered an area of ≤ 10 acres (c. 2.5 ha, Willis, 2001). The croft consists of inbye land adjacent to the croft house, which is used as pasture for both sheep and cattle, and the cultivation of crops for use by the crofters' family. In addition, as members of the township crofters have access to common grazings located on the moorland adjacent to the settlement (Stewart, 2005). In the Outer Hebrides, crofters have access to the machair in addition to the hill grazings. As with moorland grazings, this land is held in common, and provides suitable land for the majority of agricultural activities. Consequently, the majority of fodder crops are cultivated on the machair on these islands (Hance, 1952; Caird, 1979). The allocation of common grazings (both moorland and machair) throughout the Crofting Counties are administered and regulated by Grazing Clerks from each township (Willis, 2001).

Traditionally, crofters reared small numbers of sheep and cattle, and undertook small scale cropping activities which primarily consisted of cultivating fodder crops for their livestock. Livestock grazed the lowland grasslands provided by the inbye and machair during the winter and were relocated to the moorland during the summer months (Hance, 1952; Moisley, 1962; Caird, 1979; Stewart, 2005). The removal of livestock during the summer enables pasture to regenerate, whilst winter grazing creates an open sward that allows wildflowers to compete with grasses, thus increasing plant species diversity (Stewart and Pullin, 2008). The widespread use of this grazing regime, particularly by crofters on the Outer Hebrides, has resulted in the diverse wildflower assemblages characteristic of the machair and has consequently made this a valuable habitat for several of the UK's endangered insect fauna, including *B. distinguendus* (MacDonald, 2003; Benton, 2006). Traditional crofting techniques also include leaving land fallow as part of the arable rotation, a practice that is often absent from modern farming practices as the use of artificial fertilizers has removed the need to 'rest' nutrient deficient land. In contrast, crofters traditionally utilise farm yard manure and rotten seaweed as natural fertilizers to enhance the nutrient poor soils of the machair and inbye. The variety of agricultural practices employed by crofters, in conjunction with the close proximity of crofts, has created a mosaic of habitats, a landscape feature shown to promote diversity and abundance in a range of farmland species (Weibull *et al.*, 2003). Consequently, the crofted landscape supports significant populations of a number of species which have declined elsewhere in the UK, such as corn buntings (*Miliaria calandra*) and corncrakes (*Crex crex*) (Stroud, 1998; Love, 2003; Mackenzie, 2007).

Crofting largely escaped the major impacts of agricultural intensification experienced elsewhere throughout the UK and western Europe during the last century. However, crofting practices have evolved throughout this period and signs of intensification, and the

subsequent impacts on biodiversity, are now evident. The main drivers of this change in management practices are a range of socio-economic factors which are apparent throughout the Crofting Counties, and the Outer Hebrides in particular. For example, increasing house prices and the lack of skilled jobs is driving the outmigration of young people from these islands, resulting in a declining population size, an increasingly elderly population and a reduction in the number of crofters actively managing their land (Hall Aitken, 2007; Mackenzie, 2007; Comhairle nan Eilean Siar, 2009a,b). This decline in active land management has led to the ecological degradation of croft land (Crofters Commission, 1991), and the simplification of the crofting system; for instance, mixed livestock crofts are frequently replaced by sheep, which are easier to rear by elderly crofters than more labour intensive beef cattle, and many older crofters now view crofting as a purely sheep based system (Willis, 2001). The widespread production of sheep and the associated problems of overgrazing on inbye land throughout this region has significant ecological repercussions (see Chapter 2). In line with the declining population of the Crofting Counties, the number of crofting households fell by 23% during the 1950s – 1980s (Crofters Commission, 1991), and there are currently c. 17,000 registered crofts but only 10-12,000 associated households (Stewart, 2005). This has resulted in a move towards multiple tenancies, whereby one crofter is responsible for the management of several crofts simultaneously (Willis, 2001; Stewart, 2005). With fewer active crofters more intensive practices are increasingly employed to make agricultural activities more efficient and economically viable, such as the move from hay to silage production, the introduction of tractors, and the fencing and reseeded of pastures to increase grass quality (Caird, 1979; Willis, 1991). The combined effect of multiple tenancies and more efficient crofting practices are reducing landscape heterogeneity and therefore reducing the ecological value of croft land. In addition, the movement into the region of middle class families looking for a better life but who have little agricultural experience (Willis, 2001),

or, in the Outer Hebrides, foreign workers arriving to address labour shortages in non-agricultural industries are also impacting on crofting communities (Hall Aitken, 2007). The Crofting Reform Act (2007) and changes to agricultural subsidies have also affected the way in which crofts are managed. With still further changes to support planned in the near future, the outlook for crofting, and for the biodiversity that depends on active land management, is uncertain.

1.5. Research objectives

Crofting is a unique form of agriculture that is inextricably linked with the social history of the people of northern Scotland. However, traditional crofting practices are rapidly disappearing throughout the Crofting Counties in response to a range of socio-economic drivers. This has grave implications for both the persistence of crofting communities in these remote areas of Scotland, and the biodiversity that depends on the continuation of traditional croft land management practices. As with the conservation of many rare species throughout the world, the persistence of biodiversity in crofting areas is strongly associated with the future of the communities who are responsible for land-use in the region. Therefore, the aim of this research project is to determine whether it is possible to reconcile the disciplines of ecology and economics to support crofting communities in the use of environmentally beneficial land management practices and, in turn, conserve the biodiversity dependant on crofted land. In this study I focus on the rare bumblebee fauna of the Outer Hebrides and examine ways in which agricultural support through both direct government payments (*e.g.* the Single Farm Payment) and AES influence croft land management practices, and hence impact on bumblebee populations. I investigate how support systems can be modified to enable crofters to retain viable croft businesses whilst promoting or maintaining bumblebee populations, and provide recommendations for future conservation management strategies.

In order to achieve this I have four key objectives which have helped direct my research:

1. Quantify the relationship between croft land management practices and the abundance of rare bumblebees utilising croft land and adjacent non-agricultural habitats;
2. Analyse current crofting economics on machair systems;
3. Develop and calibrate socio-economic models to predict how altering subsidy payments may affect croft production decisions;
4. Formulate policy recommendations to support a crofting system that is both viable and maximises the abundance of rare bumblebee species in crofting landscapes.

I address objective 1 in chapters 2 and 3. Chapter 2 specifically examines the relationship between croft land management practices and the abundance of all bumblebee species found in the Outer Hebrides and Durness, and provides conservation management recommendations based on the results of the ecological survey work. Chapter 3 builds on the work of the previous chapter, specifically to examine the importance of adjacent non-agricultural habitats, which were highlighted as possible additional foraging habitats for bumblebees in the Outer Hebrides. To broaden the scope of my research, I also conducted a comparative survey on the Somerset Levels which are home to *B. sylvarum*, another of the UK's rarest bumblebees. Objective 2 is addressed in Chapter 5, which provides an analysis of the economics of crofting in the Outer Hebrides at present, whilst Objective 3 is considered in chapters 4 and 6. Chapter 4 provides an extensive background to the use of ecological-economic modelling in the conservation of the natural environment, whilst Chapter 6 examines the impact of conservation on the production decisions made by crofters, their impacts on croft income, land-use, and bumblebee populations. Chapter 7 consists of my final discussion and conclusions, with accompanying policy management recommendations as set out in Objective 4, and completes my thesis.

Chapter 2. Crofting and bumblebee conservation: The impact of land management practices on bumblebee populations in northwest Scotland

The work presented in this chapter is taken from the 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. The remit of this section of my project required additional help from another researcher, therefore Nicola Redpath and I undertook the research as a joint study. All the work (fieldwork, analysis and write-up) was divided and conducted by us equally. We are consequently both joint first authors of the paper and this chapter may also be found in her PhD thesis: N. Redpath. Restoration and management of wildflower-rich machair for the conservation of bumblebees. Unpublished PhD thesis, Stirling University.

2.1. 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 agriculture in this region is crofting, a system specific to Scotland in which small agricultural units (crofts) operate rotational 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.

2.2. 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 twentieth century (Robinson and 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 and 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 *B. 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 Gaelic 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 fertilizers 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 fertilizers

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 buntings (*Miliaria calandra*) and corncrakes (*Crex crex*) (Stroud, 1998; Love, 2003, Mackenzie, 2007). However, crofting communities are changing. In the Outer Hebrides, the declining population size combined with an ageing population as a result of high outward migration of the young (Mackenzie, 2007; Comhairle nan Eilean Siar, 2009a), 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 paper 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.

2.3. Methods

2.3.1. 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 (Fig. 2.1). 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 one and seven 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 2.1.

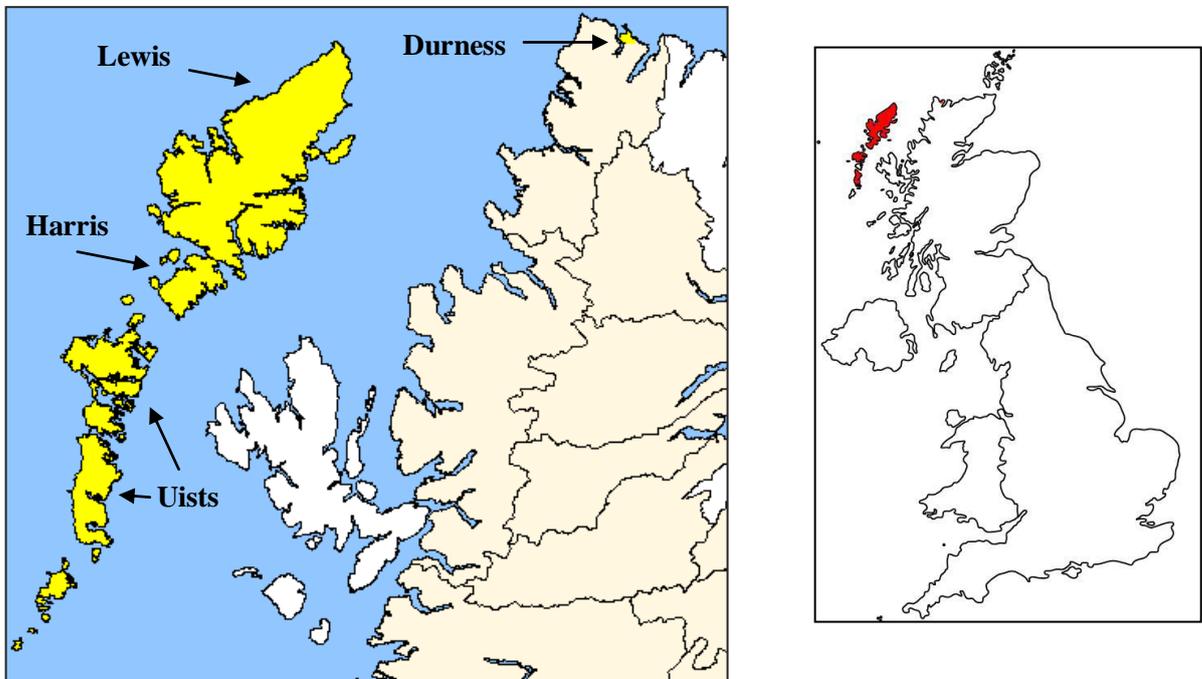


Fig. 2.1. Location map of the Outer Hebridean study sites in relation to the rest of the UK.

Table 2.1. Croft management types and their definitions with the relative range in area of each management type surveyed.

Management	Definition	Mean area of transect surveyed in m ²		
		June	July	August
Arable	Cultivated land sown with an annual crop, including mixed cereals (barley, oats & rye) and root vegetables	378	417	378
Bird and Bee Conservation Mix	A brassica-rich mix sown primarily to benefit a number of bird species and also foraging bumblebees. Contains kale, mustard, <i>phacelia</i> , fodder radish, linseed & red clover.	620	760	620
Fallow	Cultivated land that has not been seeded for one or more years	1820	1820	1820
Mixed Grazing	Land grazed throughout the year by a combination of both cattle and sheep	2800	2289	2909
Sheep Grazed	Land grazed at various times throughout the year by sheep	2372	2511	2412
Silage	Grass crop harvested whilst green and then partially fermented for livestock fodder	2257	2267	2629
Unmanaged Pasture	Formerly grazed pasture where active management has ceased	2200	2200	2200
Winter Grazed Pasture	Pasture grazed between September and May	2850	3053	2167



(a)



(b)



(c)



(d)



(e)



(f)



(g)



(h)

Plate 2.1a-h. The eight management types surveyed on crofts in the summer of 2008. Source L. Osgathorpe.
Key: (a) Arable, (b) B & B mix, (c) Fallow, (d) Mixed grazed pasture, (e) Sheep grazed pasture, (f) Silage, (g) Unmanaged pasture, (h) Winter grazed pasture.

2.3.2. 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 looped across sections at 25 m 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 m on either side of the transect 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 m of the crop side of the transect 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.

2.3.3. 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 0.5 m quadrat was positioned every 50 m 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 m 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.

2.3.4. Data analysis

The effect of croft management on bumblebee abundance was examined using generalised linear models with a quasipoisson distribution 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. A model was constructed for each month of the survey period, and a pseudo R^2 value calculated. Pair-wise comparisons between management types were conducted to assess differences in bumblebee abundance between management types within each month.

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 2.2; 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 quasipoisson errors and included crofter as a factor and transect area as an offset.

Table 2.2. The number of foraging visits made by bumblebees to each of the key forage plant species in each month of the 2008 survey period. Data shown as a percentage.

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

2.4. Results

2.4.1. Bumblebee species

A total of 246 foraging bumblebees belonging to six species were recorded on crofts throughout the survey period (Table 2.3). *B. muscorum* was the most commonly recorded species across the study area. *B. lucorum* was recorded less frequently but remained relatively common compared with *B. hortorum* and *B. distinguendus* which were both scarce. *B. jonellus* was not recorded on any crofts, although it does occur in the study areas.

The bumblebee species recorded varied between study areas. Geographic location governed the species present on some sites, such as the ‘mainland ubiquitous’ species *B. terrestris* and *B. 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. 2.2a-c), and these patterns were consistent across species. Abundance was highest in August when 58% of all bumblebee 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.

2.4.2. Croft management and bumblebee abundance

In this study 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 2.4). The effect of crofter on bumblebee abundance was significant in July and August only (Table 2.4). These models explained 22%, 70% and 47% of the variance in bee numbers in June, July and August respectively.

The utilization of each management type by foraging bumblebees varied between months (Figs. 2.2a-c). Bumblebee abundance was low in June with little variation observed between management types (Fig. 2.2a, Table 2.5). 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 9 times as many bumblebees supported by these two management types respectively in June.

In July, mixed grazing sections contained significantly fewer bumblebees than fallow, silage and winter pasture (Fig. 2.2b, Table 2.6). 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. 2.2c, Table 2.7). ‘Bird and bee’ conservation mix sections supported significantly more bumblebees than all other management types except unmanaged pasture in this month. The difference in the median number of bumblebees 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 2.7). The median number of bumblebees supported by mixed grazing and fallow was four and 16 times greater than that of sheep grazed sections (Fig. 2.2c). 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. 2.3). 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: $w = 2126.0$, $p < 0.0001$).

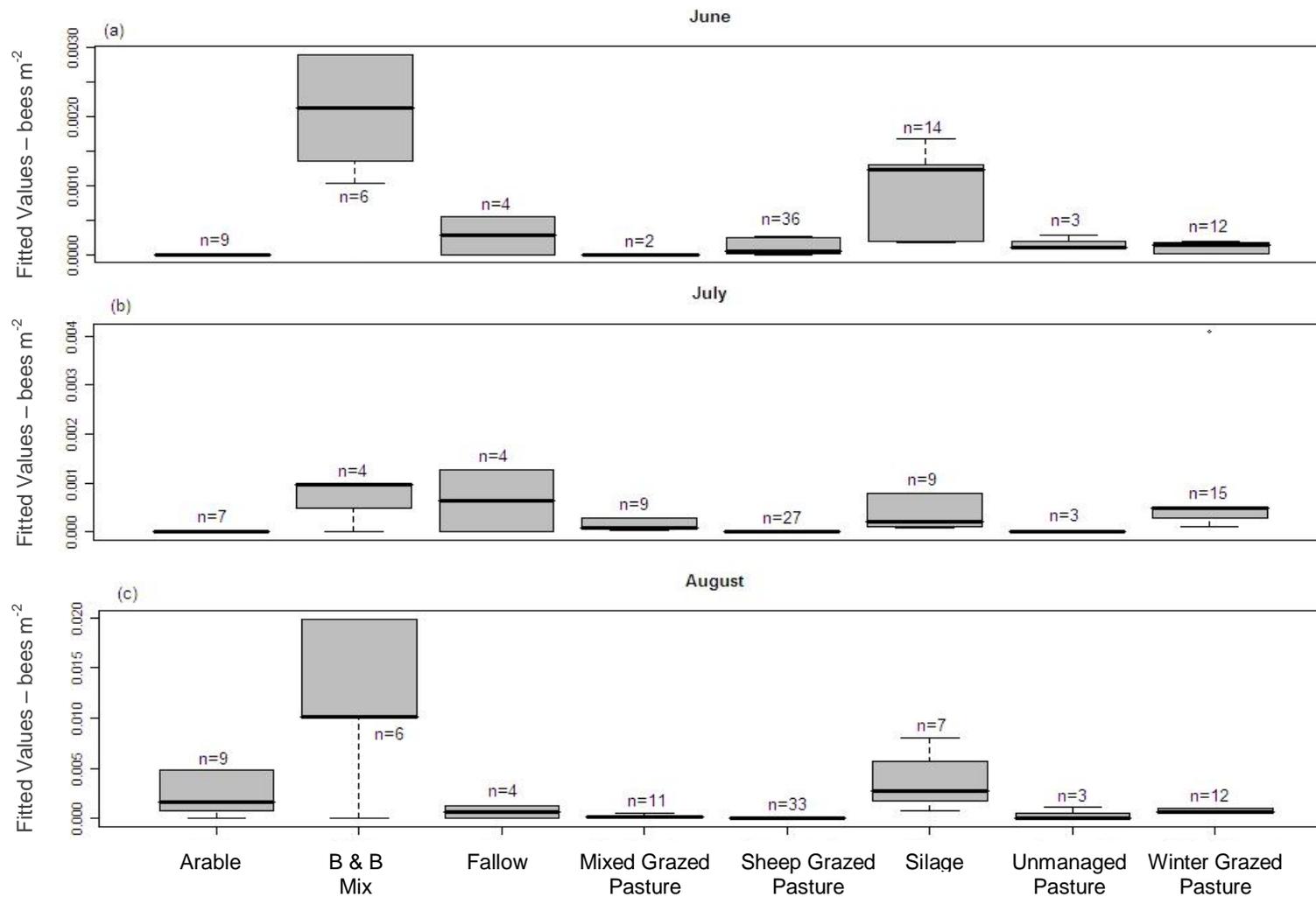
Table 2.3. The percentage of each bumblebee species (total n = 246) observed foraging on crofts across the study area in 2008.

Bumblebee Species	% Total Bumblebees
<i>B. muscorum/pascuorum</i> ²	77.2
<i>B. lucorum/terrestris</i>	19.5
<i>B. hortorum</i>	2.4
<i>B. distinguendus</i>	0.8

Table 2.4. A summary of test statistics derived from the model examining the effect of land management type and crofter on bumblebee abundance across the 2008 survey period.

Month	Factor				
	Management		Crofter		
June	$\chi^2_7 = 18.244$	p = 0.0109	$\chi^2_9 = 13.001$	p = 0.1625	n=10
July	$\chi^2_7 = 109.742$	p = <0.0001	$\chi^2_8 = 69.127$	p = <0.0001	n=9
August	$\chi^2_7 = 71.764$	p = <0.0001	$\chi^2_9 = 41.444$	p = <0.0001	n=10

² *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.



Figs. 2.2a-c. Box plots showing fitted values from the models for bumblebee abundance across eight different croft management types in June, July and August 2008 respectively. Boxes represent the location of the middle 50 percent of the data and the whiskers indicate the interquartile range of the data.

Table 2.5. Pair-comparisons for management type on bumblebee abundance in June 2008 following a GLM indicating a significant effect of management. 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.

Management Types	Arable		B & B Mix		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 ³	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	0.01	-0.767	0.45	-2.187	0.03						
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	0.02	-0.874	0.39	-2.057	0.04	-0.270	0.79	0.002	1.00	-0.740	0.46

³ B & B Mix refers to the Bird and Bee conservation mix.

Table 2.6. Pair-comparisons for management type on bumblebee abundance in July 2008 following a GLM indicating a significant effect of management. 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.

Management Types	Arable		B & B Mix		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 ⁴	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	0.01	-2.018	0.05	0.005	1.00				
Unmanaged Pasture	<-0.001	1.00	-0.002	1.00	-0.002	1.00	-0.002	1.00	1.44x10 ⁻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	4.00x10 ⁻³	1.00	2.343	0.02	0.002	1.00

⁴ B & B Mix refers to the Bird and Bee conservation mix.

Table 2.7. Pair-comparisons for management type on bumblebee abundance in August 2008 following a GLM indicating a significant effect of management. 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		Fallow		Silage		Sheep Grazed		Mixed Grazing		Unmanaged Pasture	
	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>
B & B Mix ⁵	3.298	<0.01												
Fallow	-1.792	0.08	-4.463	<0.001										
Silage	0.892	0.38	-3.727	<0.001	2.677	0.01								
Sheep Grazed	-3.281	0.01	-5.596	<0.001	-1.842	0.07	-4.104	<0.001						
Mixed Grazing	-2.824	0.01	-5.380	<0.001	-1.069	0.29	-3.845	<0.001	0.963	0.34				
Unmanaged Pasture	0.205	0.84	-1.875	0.07	1.116	0.27	-0.182	0.86	2.311	0.02	1.744	0.09		
Winter Pasture	-1.152	0.25	-4.535	<0.001	0.825	0.41	-2.507	0.01	2.897	0.01	2.187	0.03	-0.743	0.46

⁵ B & B Mix refers to the Bird and Bee conservation mix.

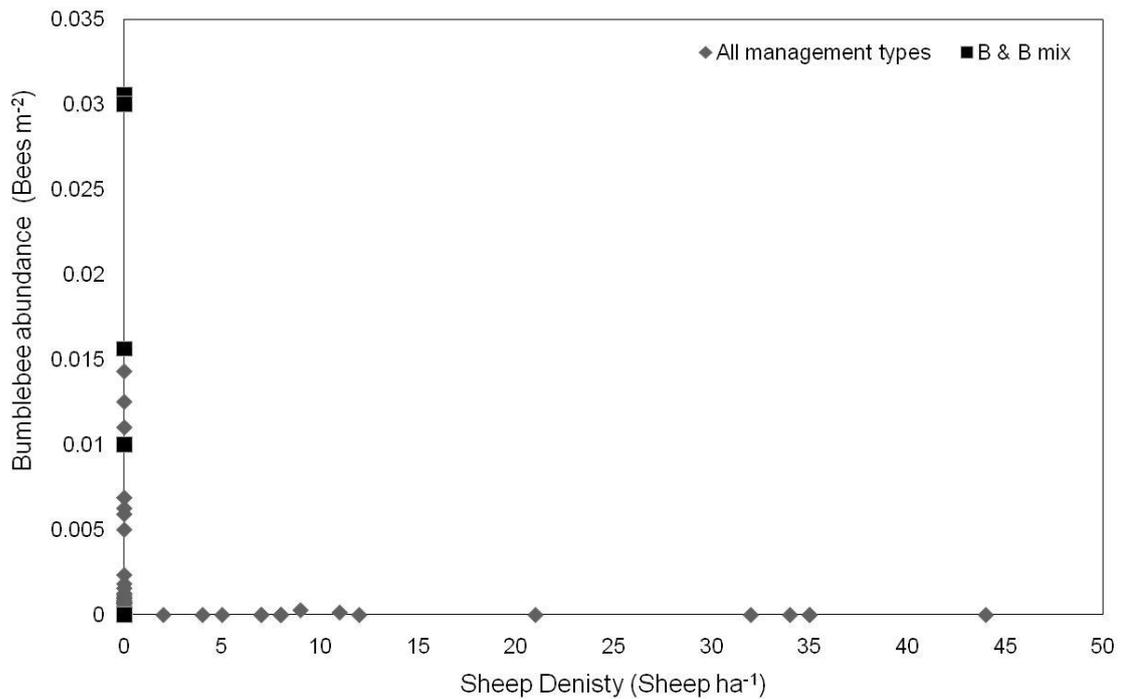


Fig. 2.3. The relationship between the density of grazing sheep and the relative abundance of foraging bumblebees on crofts in August 2008. The data points for the Bird & Bee conservation seed mix (B & B mix) are shown separately. The pattern was identical for June and July.

2.4.3. 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. 2.4c). However, the density of inflorescences recorded per quadrat was considered to be low throughout the season (<15 flowers quadrat⁻¹ in June and July, <25 flowers quadrat⁻¹ in August). There was a significant effect of management type on inflorescence availability in June and in July (Tables 2.8, 2.9, 2.10). Crofter was only significant in June and August (Table 2.8). 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 2.4a-c, Table 2.11). Consequently, the effect of management type on the availability of forage plants was not significant in August (Table 2.8). 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 between forage plants and land management type was broadly similar to that observed in July.

2.4.4. The relationship between bumblebee abundance and forage plant availability

The relationship between the number of bumblebees and flowers varied throughout the survey period in line with the temporal availability of foraging resources. June was a particularly poor month for flowering plants across the study area due to a prolonged period of unusually dry weather in the preceding months, and the number of bumblebees per croft section did not vary significantly with flower abundance ($\chi^2 = 0.27_1$, $p = 0.602$). Floral abundance increased in July and August across the study area and inflorescence availability became a significant predictor of bumblebee abundance in both months ($\chi^2 = 8.30_1$, $p = 0.004$ in July, $\chi^2 = 10.67_1$, $p = 0.001$ in August). The amount of variation in bumblebee abundance explained by these models was low (all R^2 values were $< 10\%$), indicating that models using management type and crofter are a better predictor of bumblebee abundance across the study area.

2.4.5. Bumblebee forage plants

The floral resources utilised by foraging bumblebees varied throughout the season (Table 2.2). 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.

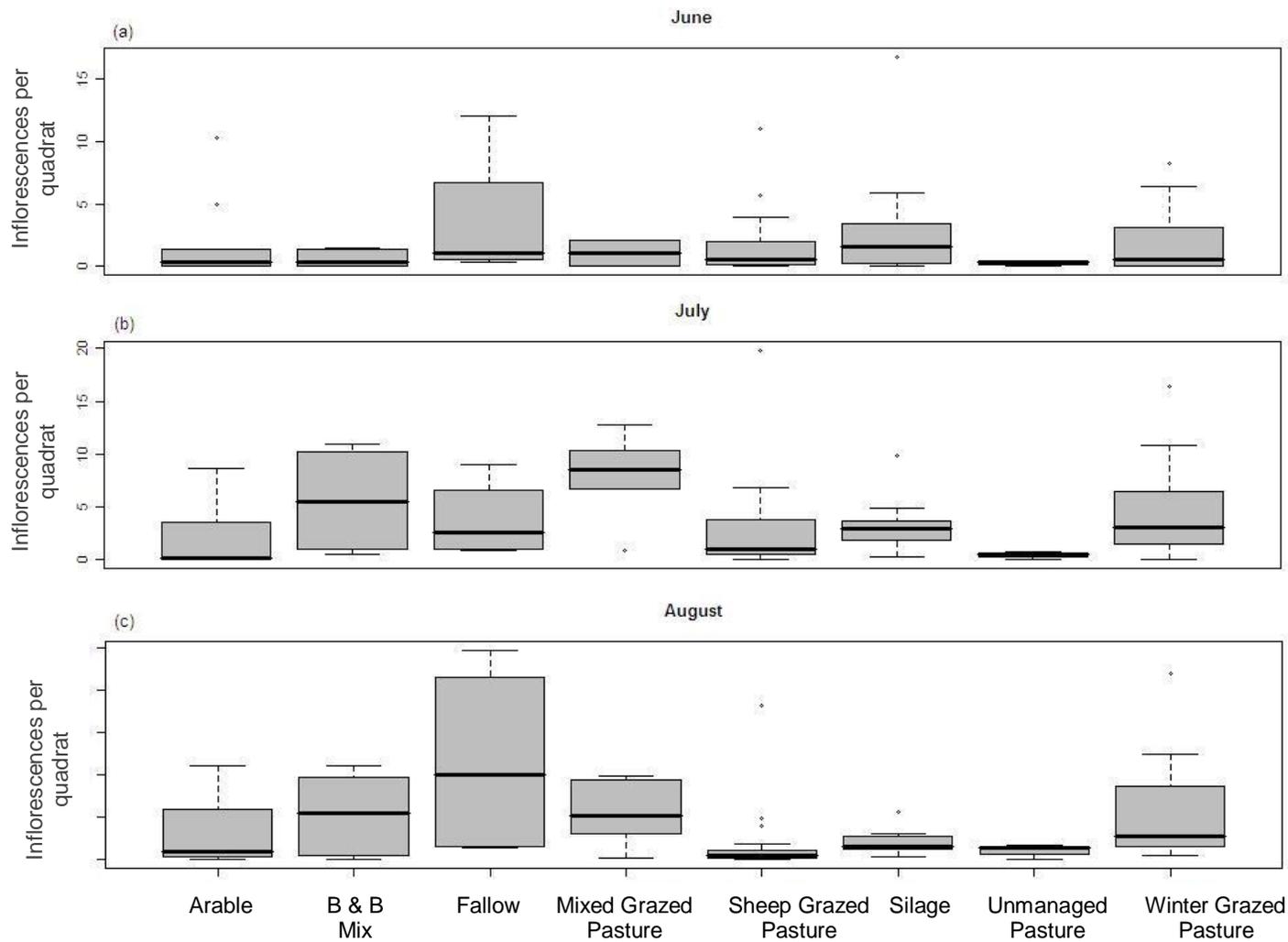
Visits to white clover declined in July to 33% although it still remained the most frequently visited species and its abundance remained greatest on sheep grazed sections where 63% of this species was recorded. The use of other species increased during July, particularly those belonging to the Fabaceae. Red clover (*T. 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 2.2). 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. However, 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.

Table 2.8. A summary of test statistics derived from the model examining the effect of land management type and crofter on the abundance of bumblebee forage plant inflorescences across the 2008 survey period.

Month	Factor			
	Management		Crofter	
June	$\chi^2_7 = 25.140$	p = 0.0007	$\chi^2_9 = 13.001$	p = <0.0001
July	$\chi^2_7 = 17.815$	p = 0.0128	$\chi^2_8 = 10.237$	p = 0.2488
August	$\chi^2_7 = 5.5588$	p = 0.5921	$\chi^2_9 = 31.563$	p = 0.0002



Figs. 2.4a-c. Box plots showing variation in the abundance of forage plants across eight different croft management types in June, July and August 2008 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 interquartile range of the data.

Table 2.9. Pair-comparisons for management type on floral abundance in June 2008 following a GLM indicating a significant effect of management. 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.

Management Types	Arable		B & B Mix		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 ⁶	-0.933	0.35												
Fallow	-0.555	0.58	0.135	0.89										
Silage	2.124	0.04	2.557	0.01	1.699	0.09								
Sheep Grazed	0.023	0.98	1.128	0.26	0.593	0.56	-3.316	<0.01						
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

⁶ B & B Mix refers to the Bird and Bee conservation mix.

Table 2.10. Pair-comparisons for management type on floral abundance in July 2008 following a GLM indicating a significant effect of management. 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.

Management Types	Arable		B & B Mix		Fallow		Silage		Sheep Grazed		Mixed Grazing		Unmanaged Pasture	
	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>
B & B Mix ⁷	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

⁷ B & B Mix refers to the Bird and Bee conservation mix.

Table 2.11. Pair-comparisons for management type on floral abundance in August 2008 following a GLM indicating a significant effect of management. 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.

Management Types	Arable		B & B Mix		Fallow		Silage		Sheep Grazed		Mixed Grazing		Unmanaged Pasture	
	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>
B & B Mix ⁸	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

⁸ B & B Mix refers to the Bird and Bee conservation mix.

2.5. 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 and their forage plants 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 (L. Osgathorpe and N. Redpath, 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.

2.5.1. 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 and 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 densities, 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.

2.5.2. 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 moorlands 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 key 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 and Tiainen, 2002; Westphal *et al.*, 2006). Successional sowings of conservation seed mixes may achieve this lengthy flowering period (Carreck and 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, *Parotapion ryei*, another UK BAP invertebrate species which has a stronghold in the Outer Hebrides but is classified as nationally scarce, relies on red clover as a larval food source and therefore promoting clover rich seed mixes for the conservation of bumblebees may be of benefit to populations of 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.

2.5.3. *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 (AES) tailored specifically for low-intensity systems. However, 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 and Tiainen, 2002; Goulson and 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 AES. 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.

Chapter 3. The use of off-farm habitats by foraging bumblebees in agricultural landscapes: Implications for conservation management

The work presented in this chapter forms the basis of the paper: Osgathorpe, L.M., Park, K., Goulson, D. The use of off-farm habitats by foraging bumblebees in agricultural landscapes: Implications for conservation management. Apidologie. In press.

3.1. Abstract

Recent studies have focused on ways to enhance floral availability on arable farmland, but little attention has been paid to the importance of off-farm habitats in providing forage for pollinators within farmed landscapes. I conducted a comparative study to assess bumblebees and flower abundance on farmed and off-farm habitats in two low-intensity systems in the UK. I show that road verges and track edges provide forage and attract long-tongued bumblebees in both farming systems. Also, grazing management depends on the farming system in operation, with cattle grazing providing a valuable foraging habitat for short-tongued bumblebees in southwest England. Therefore, to conserve bumblebees in agricultural landscapes the type of farming system needs to be taken into account in developing grazing management regimes, whilst non-agricultural habitats need to be integrated into local land management plans to ensure the provision of forage for bumblebees throughout the breeding season.

3.2. Introduction

Agriculture is the dominant land use in the EU (Robinson and Sutherland, 2002), and accounted for 77% of the UK's total land use in 2007 (DEFRA, 2007). Agricultural intensification throughout the second half of the twentieth century has frequently been identified as the primary driver behind declines in farmland biodiversity in the UK and

western Europe (Chamberlain *et al.*, 2000; Robinson and Sutherland, 2002). Increasing mechanisation, the conversion of semi-natural grasslands to arable land, and larger farm unit sizes has led to the loss and degradation of many semi-natural habitats and an increasingly homogenous agricultural landscape (Stoate *et al.*, 2001; Benton, 2006).

Such intensification of land-use has resulted in declines of many species of flora and fauna, particularly habitat specialists (Robinson and Sutherland, 2002). Consequently, many species now found in farmland habitats are generalists that have been able to adapt to the changes in environmental conditions. This has been observed across different groups including birds, butterflies, plants (Robinson and Sutherland, 2002), and bumblebee populations throughout the UK and Europe (Goulson *et al.*, 2005; Goulson, *et al.*, 2006). Of the 25 bumblebee species native to Britain, three are now extinct and seven others are formally listed as being threatened (Benton, 2006; Goulson *et al.*, 2008a). As relatively long range foragers they are able to utilise a wide range of different foraging habitats, therefore landscape context as well as heterogeneity are important factors influencing their abundance and richness in agricultural areas (Rundlöf *et al.*, 2008). Bumblebees are most commonly associated with wildflower rich semi-natural grasslands and heathland habitats (Goulson, 2003a; Williams and Osborne, 2009). However, vast areas of these semi-natural habitats have been lost over the past century following changes to agricultural practices, as illustrated by the loss of unimproved lowland grassland which is estimated to have declined by over 90% between 1932 and 1984 in the UK (Fuller, 1987). Consequently, intensive farming in the south, east and centre of the UK has reduced bumblebee density and diversity (Williams and Osborne, 2009), and resulted in a ‘central impoverished area’ where only the six most common species are frequently found (Williams, 1982). The rarest bumblebees are now confined to isolated areas that have not received the high levels of agricultural intensification experienced elsewhere in the UK (Goulson *et al.*, 2006).

Two examples of such areas are the crofting systems found in northwest Scotland and the Somerset Levels in southwest England.

Agriculture in crofting areas traditionally operated on a small scale, with few artificial inputs. Traditional crofting practices include areas of lowland grassland grazed during the winter months and livestock relocated to moorland grazings during the summer. Consequently, crofted areas often provide suitable habitats for many species that are rare elsewhere in the UK (e.g. corncrake [*Crex crex*], northern colletes bee [*Colletes floralis*]; Love, 2003). The flower rich machair grasslands found along the west coast of the Outer Hebrides in Scotland are particularly important, providing floral resources for a wide range of invertebrates including *B. distinguendus* and *B. muscorum* (Goulson *et al.*, 2005; Benton, 2006).

The Somerset Levels and Moors Environmentally Sensitive Area (ESA) covers over 27,000 ha of central Somerset and is characterised by low-lying, traditionally managed wet and open grassland bounded by drainage ditches ('rhynes') and bisected by trackways, locally known as 'droves' (Natural England, 2010). The grassland landscape consists of species rich meadows and pastures (Natural England, 2010), which provide foraging habitats for at least 15 species of bumblebee, including the rare *B. sylvarum* and *B. ruderarius* (Benton, 2006). In common with the crofted areas of the Outer Hebrides, the Somerset Levels are sparsely populated, with human settlements clustered together on ridges and higher ground (Natural England, 2010). Agriculture is typified by beef and dairy farming, although under the former ESA scheme management restrictions were imposed to preserve the ecological integrity of the region.

The agricultural systems in operation in northwest Scotland and southwest England may superficially appear very different, however, traditionally they both provide essential grassland foraging habitats for bumblebees and internationally important habitats for many other taxa (Love, 2003; Natural England, 2010). However, whilst much of the Somerset Levels are under the influence of positive conservation management, crofting practices in Scotland are changing, with increasing flock sizes and an increase in the use of lowland grasslands (inbye) for sheep grazing in summer (Willis, 1991; Sutherland and Bevan, 2001). These changes can render the inbye of low value to foraging bumblebees (Chapter 2). This is of major concern given the nationally important bumblebee populations found in the Outer Hebrides.

The value of non-agricultural habitats, such as road verges and tracks, to invertebrates in farmed landscapes has been examined by several authors (*e.g.* Croxton *et al.*, 2002; Hopwood, 2008; Noordijk *et al.*, 2009). In less intensively managed farmland areas of Estonia greater bumblebee diversity was recorded foraging on these off-farm habitats compared to farmed habitats (Mänd, *et al.*, 2002). In Chapter 2 I provide anecdotal evidence of the use of such habitats by foraging bumblebees in crofted areas, and suggest that these may be of importance in supporting bumblebee populations in the Outer Hebrides, Scotland. In this chapter I conduct a comparative study between two grassland based farming systems in the UK to determine the value of off-farm habitats to foraging bumblebees in a system threatened by agricultural intensification and one which remains less intensively managed.

3.3. Methods

3.3.1. Study sites

I conducted my study in the Outer Hebrides and the Somerset Levels in two consecutive years to enable me to compare the importance of farm versus off-farm habitats for bumblebees. In 2009, fieldwork was undertaken on the island of North Uist in the Outer Hebrides. Survey work focused on the habitats surrounding the crofting townships of Balranald, Hougharry and Tigharry in the northwest of the island (N 57°36'20.12", W 7°30'33.27"), which cover an area of approximately 5 km². Within this area six different habitats were identified which included all of the major habitats present: silage, fallow, summer grazed pasture (mixed livestock), winter grazed pasture, road verges, and track edges. Road verges refer to the grassy embankments found along public highways, whereas track edges refer to the edge habitats bordering rough, un-surfaced tracks with low vehicle use.

In 2010, I concentrated my study on habitats characteristic of the Somerset Levels, focusing on a 5 km² area south and west of the villages of Cheddar, Draycott and Rodney Stoke (N 51°15'17.95", W 2°46'35.50"). I identified four different habitats within this area which represented all the major habitats present: silage, cattle grazed pasture, road verges, and track edges. Habitat types and their definitions are listed in Table 3.1.

3.3.2. Bumblebee sampling techniques

Bumblebee surveys were carried out on each habitat between the 27th July and 15th August 2009 in the Outer Hebrides, and between 9th June and 16th August 2010 on the Somerset Levels. Six replicate sections of each habitat (except summer grazed pasture) were identified and separated from one another by a minimum distance of 100 m. In most instances, agricultural sections were equivalent to a field. Due to access restrictions I was

only able to survey five sections of summer grazed pasture in 2009. In the Outer Hebrides, track edges, winter grazed pasture, fallow and arable habitats were all located on the machair, with summer grazed pasture located on the inbye land associated with the crofts. Each individual section was surveyed once for foraging bumblebees in August 2009 in the Outer Hebrides. In 2010, I extended the survey throughout the summer and surveyed each section three times, once in June (9th -15th), and again in July (12th – 19th) and August (9th – 16th).

Surveys, or ‘bee walks’ were conducted along a series of line transects that were randomly distributed throughout each habitat. In fields (*i.e.* sections of pasture) transects were conducted along a zig-zag route to ensure that a representative area of the habitat was surveyed. All foraging bumblebees observed within 2 m on either side of the transect were recorded and identified to species and caste level. The plant species on which bumblebees were observed foraging were also recorded. On the Somerset Levels silage sections were inaccessible prior to the first cut in June, therefore these sections were surveyed in July and August only. In the Outer Hebrides, silage is cut later in the year and the boundaries of the crop stands were accessible. Consequently, transects were relocated to run parallel with two perimeter edges of the crop forming an ‘L’ shaped transect. All bumblebees observed foraging within 2 m of the crop side of the transect were recorded, in addition to the forage plant species being utilised. This survey methodology is based on that utilised in Chapter 2 where I surveyed bumblebees in similar habitats in 2008.

In linear habitats (road verges and track edges) the method of bumblebee sampling was adapted from the standard butterfly monitoring protocols developed by Pollard (1977). Linear transects were undertaken on randomly selected areas of habitat and walked in one direction along the adjacent road/track. One side of the linear feature was selected

randomly for survey as was the direction the transect was walked in. Bumblebees observed foraging within 2 m of the selected side of the transect were recorded as previously described.

All surveys took place in dry weather and when the temperature was above 12°C. The number and species of any livestock present along a transect were also recorded.

3.3.3. Forage plant sampling techniques

The abundance of bumblebee forage plants in the different habitats was determined by conducting a survey of bumblebee forage plants across the same replicate sections as used for the bee walks using a 0.5 m x 0.5 m quadrat. The number of quadrats taken in each section was proportional to the section area, with a total of 200 quadrats per habitat. The location of each quadrat was determined using coordinates derived from a random number generator. To reduce potential crop damage silage sections in the Outer Hebrides were surveyed from a transect which ran along two adjacent edges of the crop. In this instance, the number of quadrats per section of silage habitat was proportional to the length of the transect. Although quadrats were placed within the crop they were limited to the edge of the habitat and therefore may not be representative of whole habitat area. Each habitat section was sampled once during the survey period in 2009 in the Outer Hebrides, and once each month between June – August 2010 on the Somerset Levels to correspond with the monthly bee walks. The inflorescences of all flowers which are utilized by foraging bumblebees were recorded, as Chapter 2.

Table 3.1. Habitats and their definitions with the range in area of each habitat surveyed in 2010.

Habitat	Definition	Transect area surveyed (m ²)	
		Outer Hebrides	Somerset Levels
Silage	<ul style="list-style-type: none"> Outer Hebrides: cultivated land sown with a grass crop or mixed cereals (barley, oats & rye). Somerset Levels: land left to regenerate to form a natural grass crop/ grazed for a short period after cutting. 	400 - 600	1372 - 2568
Fallow	<ul style="list-style-type: none"> Cultivated land, not seeded for ≥ 1 years. 	1200 - 3700	0
Pasture	<ul style="list-style-type: none"> Outer Hebrides: land grazed throughout the year by sheep, cattle or both. 	1000 - 3200	172 - 2900
Cattle Grazed Pasture	<ul style="list-style-type: none"> Somerset Levels: land grazed by cattle throughout the year. 		
Winter Pasture	<ul style="list-style-type: none"> Outer Hebrides: land grazed between September and May. 	800 - 6000	0
Track Edges	<ul style="list-style-type: none"> Outer Hebrides: track edges traversing the machair grassland. No formal management, often ungrazed during the summer due to close proximity to fallow and arable habitats. Somerset Levels: tracks providing farm access to cattle and silage fields, often bounded by rhynes (drainage ditches) and hedges. 	500 - 1300	700 - 1300
Road Verges	<ul style="list-style-type: none"> Land forming the verge of public highways, 2 m either side of the highway. Outer Hebrides: No known management Somerset Levels: One cut between the June and July surveys. 	700 - 1700	840 - 1100

3.3.4. Data analysis

3.3.4.1. Bumblebee dataset

The effect of habitat on bumblebee abundance was examined using generalised linear models in the statistical software package R 2.11.1 (The R Foundation, 2010). The abundance of foraging bumblebees was examined using subsets of the data. Previous authors have found that species with longer tongues tend to be more specialised in their foraging preferences and are often rarer than species with shorter tongues (Goulson and Darvill, 2004; Goulson *et al.*, 2005; Goulson *et al.*, 2008a). For statistical analysis I grouped together long-tongued species (*B. distinguendus*, *B. muscorum*, *B. pascuorum* and *B. hortorum*) and short-tongued species (*B. lapidarius*, *B. lucorum*, *B. terrestris*, *B. jonellus*, *B. pratorum*, *B. barbutellus* and *B. sylvestris*). As very few males were recorded in either study area, species were only subdivided by tongue length for analysis and not by caste. The Outer Hebrides and Somerset Levels datasets were analysed separately. All models used quasipoisson errors except the July short-tongued bumblebee dataset where Poisson errors were utilised. Date, wind speed and temperature were included in the initial models as covariates and habitat as a fixed factor with non-significant factors eliminated through a step-wise process. Transect area was included as an offset in each model to correct for the differences in the total area surveyed in each habitat, and a pseudo R^2 value (hereafter referred to as R^2 values) calculated, by correlating the values predicted by each model with the observed data (Zuur *et al.*, 2009). Where the model indicated that habitat was a significant factor pair-wise comparisons between habitats were conducted to assess differences in bumblebee abundance between habitats within each month.

3.3.4.2. Forage plant dataset

The availability of forage was examined using generalised linear models as described above. One model using quasipoisson errors was constructed for the Outer Hebridean

dataset and Gaussian errors were utilised in the Somerset Levels model. Separate models for June, July and August were created for the Somerset Levels dataset and R^2 values were calculated for each model. The effect of habitat was examined in relation to the number of bumblebee forage plant inflorescences per section. Analyses were restricted to known bumblebee forage plants (Goulson and Darvill, 2004; Redpath *et al.*, 2010), and included any additional species which I observed bumblebees foraging upon.

The relationship between bumblebee abundance and forage availability was examined using a generalised linear model for each month of the survey, using quasipoisson errors and area as an offset except for the July short-tongued bumblebee sub-set in which Poisson errors were utilised.

3.4. Results

3.4.1. Habitat and bumblebee abundance

3.4.1.1. Outer Hebrides

A total of 494 foraging bumblebees belonging to five species were recorded across all habitat types in 2009. All species known to be found within the Outer Hebrides study area were recorded foraging in at least one of the habitats surveyed. *B. muscorum* was by far the most abundant species present, accounting for 61% of all observations. *B. lucorum* comprised 29% of observations and the remaining 10% consisted of *B. distinguendus* (7%), *B. hortorum* (3%) and *B. jonellus* (<1%).

The abundance of long-tongued bumblebees varied significantly between habitat types ($\chi^2 = 12.35$, $p = 0.03$; Table 3.2.; Fig. 3.1a). Following model simplification only habitat remained in the final model, explaining 81% of variation. Significantly fewer long-tongued bumblebees were observed in arable and pasture that was grazed throughout the

year than any of the other habitats surveyed (Table 3.2). When comparing the median number of bumblebees observed, nine times fewer were supported by arable, and four to five times fewer by pasture. There was little difference in bumblebee density between any of the other habitats.

The abundance of short-tongued bumblebees was highest on track edges and fallow habitats; however, these differences were not statistically significant ($\chi^2_5 = 5.25$, $p = 0.386$; Fig. 3.1b).

3.4.1.2. Somerset Levels

A total of 439 foraging bumblebees of nine species were recorded across all habitats in the study area between June and August (Table 3.3). Early in the season abundance was low but increased fivefold in July when flower abundance was at its peak.

Differences in long-tongued bumblebee abundance between habitats in June were small and not significant ($\chi^2_2 = 0.02$, $p = 0.992$). Higher wind speeds correlated negatively with the abundance of this group in June ($\chi^2_1 = 4.39$, $p = 0.036$), with the highest abundances recorded when wind speeds were $<1 \text{ ms}^{-1}$. Cattle grazed pasture supported 50-60% more foraging short-tongued bumblebees than road verges or track edges in June, although the differences were not significant (Fig. 3.2a).

Habitat was a significant predictor of long-tongued bumblebee abundance in July ($\chi^2_3 = 42.95$, $p < 0.0001$; Fig. 3.2b), with the model explaining 85% of the variation observed. Road verges and track edges supported significantly more long-tongued bumblebees than either cattle grazed pasture or silage fields, with nine times more bumblebees recorded on off-farm habitats (Table 3.4). Temperature was also a significant predictor of abundance

($\chi^2_1 = 9.27$, $p = 0.002$), with higher temperatures corresponding to lower abundance. No long-tongued bumblebees were recorded at temperatures above 25°C, with all observations made when the temperature was between 21.6 – 24.9°C.

The association between habitat and short-tongued bumblebee abundance in July contrasted to that of long-tongued bumblebee abundance. Cattle grazed pasture supported 50 – 60% higher densities of foraging short-tongued bumblebees than road verges or track edges. Twice as many short-tongued bumblebees were recorded on silage than either off-farm habitat ($\chi^2_3 = 22.65$, $p = <0.0001$; Fig. 3.3b; Table 3.5) and 35% of the observed variation was explained by the model. Higher wind speeds and temperatures were associated with lower densities of this group ($\chi^2_1 = 10.83$, $p = 0.001$; $\chi^2_1 = 7.44$, $p = 0.006$).

Overall, the abundance of both long- and short-tongued bumblebees declined more than fivefold between July and August, with just 51 individuals recorded across all habitats in August. However, as in July, road verges supported the greatest densities of long-tongued bumblebees, with 39% more than on silage or cattle grazed pasture ($\chi^2_3 = 10.96$, $p = 0.012$; Fig. 3.2c). Again, higher temperatures were associated with lower abundance of this group ($\chi^2_1 = 10.96$, $p = 0.038$).

There was little variation in short-tongued bumblebee abundance in August (Fig. 3.3c), and habitat had no significant association with the abundance of this group ($\chi^2_3 = 5.76$, $p = 0.124$). Wind speed was negatively correlated with abundance and was the only significant explanatory for short-tongued bumblebee abundance in this month ($\chi^2_1 = 3.84$, $p = 0.050$).

3.4.2. *Habitat and the availability of bumblebee forage plants*

The variation in the abundance of beeflower inflorescences between habitats in the Outer Hebrides is similar to that of long-tongued bumblebees, with forage availability greatest on road verges, track edges and winter grazed pasture ($\chi^2_5 = 23.2$, $p = 0.0003$; Table 3.6). Arable and summer grazed pasture had the lowest densities of bumblebee forage with fewer than 10% of total beeflowers inflorescences recorded in each habitat, less than a third of the number of inflorescences found in road verges. Unsurprisingly, arable and summer grazed areas were also the habitats where the lowest long-tongued bumblebee densities were recorded. Interestingly, fallow habitats contained significantly fewer inflorescences than road verges (Table 3.6), yet supported equal numbers of foraging long-tongued bumblebees. Although fallow contained few beeflowers it had the highest abundances of both *Senecio jacobaeae* and *Cirsium vulgare*, which were two of the most frequently visited plant species by long-tongued bumblebees.

On the Somerset Levels, forage availability was similar between habitats in June ($\chi^2_2 = 3.80$, $p = 0.150$; Fig 3.4a). In July, road verges supported significantly fewer beeflowers than either silage and cattle grazed pasture ($t = 2.19$, $p = 0.041$, $t = -2.83$, $p = 0.011$ respectively; Fig. 3.4b), with <50% of inflorescences present in either farmed habitat. No other significant differences were identified between habitats in July and no significant differences were noted in August.

3.4.3. *The relationship between bumblebee abundance and forage availability*

In the Outer Hebrides, the abundance of both long- and short-tongued bumblebees was positively correlated with the availability of bumblebee forage material but was only significant for long-tongued bumblebees ($\chi^2_1 = 4.75$, $p = 0.029$), explaining 64% of the variation observed. This is considerably less than for the model using habitat as the

explanatory variable, suggesting that habitat is a better predictor of long-tongued bumblebee abundance.

On the Somerset Levels the relationship between forage availability and bumblebee abundance varied between months and between long- versus short-tongued bumblebees. There was a positive association between the number of inflorescences and long-tongued bumblebee abundance in both June and August ($\chi^2_{1}= 27.61, p = <0.0001$; $\chi^2_{1}= 4.28, p = 0.039$ respectively), but not in July ($\chi^2_{1}= 1.01, p = 0.906$). Similarly, there was a positive association between the number of inflorescences and short-tongued bumblebees in July and August ($\chi^2_{1}= 19.22, p = <0.0001$; $\chi^2_{1}= 10.90, p = 0.001$), but not in June ($\chi^2_{1}= 0.22, p = 0.640$). In general, habitat was a better predictor of both long- and short-tongued bumblebee abundance than numbers of flowers.

3.4.4. Bumblebee forage plant choices

A total of 10 flowering plant species were utilised by foraging bumblebees throughout the study in the Outer Hebrides (Table 3.7). Of these, *Centaurea nigra*, *S. jacobae* and *C. vulgare* were the most frequently visited and together accounted for over 85% of all foraging visits recorded. *C. nigra* was most frequently recorded on winter grazed pasture (48% of records) and road verges (41% of records), and accounted for the greatest proportion of foraging visits made by *B. distinguendus* and *B. muscorum* (58% and 50% respectively). The density of *C. nigra* was a significant predictor of long-tongued bumblebee density ($\chi^2_{1}= 11.10, p = 0.0008, R^2 = 0.80$), but not of short-tongued bumblebees ($\chi^2_{1}= 2.11, p = 0.146$). The abundance of *S. jacobae* and *C. vulgare* had no significant effect on either long- or short-tongued bumblebee abundance.

In contrast, few visits were made to the Asteraceae by foraging bumblebees on the Somerset Levels (Table 3.7). *Trifolium repens* was particularly important to short-tongued species and was the most frequently utilised flower species in June and July, accounting for 90% and 60% of all foraging visits respectively. It was also a significant predictor of *B. lapidarius* abundance in July ($\chi^2_1 = 10.40$, $p = 0.001$). Summer grazed pasture and silage fields supported the greatest abundances of *T. repens* throughout the survey period. Members of the Fabaceae were also important for long-tongued bumblebees in June, although this group were predominantly recorded foraging on *Rubus fruticosus* and *Epilobium spp.* throughout the remainder of the survey period. These species were both confined to road verges and track edges, although the availability of *R. fruticosus* was similar between both habitats, whilst *Epilobium spp.* were almost exclusively located along track edges.

Table 3.2. The association between habitat on long-tongued bumblebee abundance in the Outer Hebrides in 2009. The t and p values are derived from pair-wise comparisons made between each habitat. Negative t values show that the habitat listed along the rows of the table supported significantly fewer long-tongued bumblebees than the habitat listed as the column heading, and vice versa. Numbers in bold refer to significant results at the <0.05 significance level.

	Arable		Fallow		Pasture		Road Verges		Track Edges	
	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>
Fallow	1.058	0.299								
Pasture	0.085	0.932	-1.764	0.088						
Road Verges	1.149	0.260	0.315	0.755	1.871	0.072				
Track Edges	1.246	0.223	0.584	0.564	1.985	0.057	0.276	0.785		
Winter Grazed	1.386	0.176	1.198	0.241	2.417	0.022	0.657	0.516	0.252	0.803

Table 3.3. The percentage of each bumblebee species (total n = 439) observed foraging across all habitats on the Somerset Levels throughout the field season.

Species	Tongue Length	% Total Bumblebees		
		June	July	August
<i>B. lapidarius</i>	Short	27	53	43
<i>B. lucorum/terrestris</i> ^a	Short	33	26	8
<i>B. pascuorum</i>	Long	26	14	49
<i>B. pratorum</i>	Short	11	0	0
<i>B. sylvestris</i>	Short	3	<1	0
<i>B. hortorum</i>	Long	0	5	0
<i>B. jonellus</i>	Short	0	<1	0
<i>B. barbutellus</i>	Short	0	<1	0
Unidentified	-	0	<1	0

^a Due to the difficulty in distinguishing the workers of these species from one another, individuals of both species were recorded collectively.

Table 3.4. The association between habitat and long-tongued bumblebee abundance on the Somerset Levels in July and August 2010. The t and p values are derived from pair-wise comparisons made between each of habitat. Negative t values show that the habitat listed along the rows of the table supported significantly fewer long-tongued bumblebees than the habitat listed as the column heading, and vice versa. Numbers in bold refer to significant results at the <0.05 significance level.

Habitat	July						August					
	Cattle Grazed		Road Verge		Track Edge		Cattle Grazed		Road Verge		Track Edge	
	t	p	t	p	t	p	t	p	t	p	t	p
Road Verge	2.63	0.016					1.06	0.304				
Track Edge	2.84	0.011	0.623	0.541			1.63	0.120	0.89	0.386		
Silage	0.311	0.759	-3.81	0.001	-3.97	0.001	-0.90	0.382	-2.09	0.050	-2.60	0.018

Table 3.5. The association between habitat and short-tongued bumblebee abundance on the Somerset Levels in July 2010. The z and p values are derived from pair-wise comparisons made between each of habitat. Negative z values show that the habitat listed along the rows of the table supported significantly fewer short-tongued bumblebees than the habitat listed as the column heading, and vice versa. Numbers in bold refer to significant results at the <0.05 significance level.

Habitat	July					
	Cattle Grazed		Road Verge		Track Edge	
	<i>z</i>	<i>p</i>	<i>z</i>	<i>p</i>	<i>z</i>	<i>p</i>
Road Verge	-2.23	0.026				
Track Edge	-3.02	0.003	-0.88	0.377		
Silage	1.33	0.184	3.63	0.0001	4.15	<0.0001

Table 3.6. The association between habitat and forage plant abundance in the Outer Hebrides in 2009. The t and p values are derived from pair-wise comparisons made between each of habitat. Negative t values show that the habitat listed along the rows of the table supported significantly fewer bumblebees than the habitat listed as the column heading, and vice versa. Numbers in bold refer to significant results at the <0.05 significance level.

	Arable		Fallow		Pasture		Road Verges		Track Edges	
	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>	t	<i>p</i>
Fallow	0.788	0.437								
Pasture	-0.193	0.849	-0.974	0.339						
Road Verges	3.079	0.005	2.486	0.020	3.200	0.004				
Track Edges	2.497	0.019	1.833	0.078	2.639	0.014	-0.729	0.47		
Winter Grazed	2.428	0.022	1.757	0.091	2.572	0.016	-0.811	0.425	-0.083	0.935

Table 3.7. The flower species visited by foraging bumblebees in the Outer Hebrides and the Somerset Levels. The number of visits made by long and short-tongued bumblebees to each species are shown as percentages.

Flower Species	Family	Outer Hebrides		Somerset Levels					
		Long %	Short %	June		July		August	
				Long %	Short %	Long %	Short %	Long %	Short %
<i>Centaurea nigra</i>	Asteraceae	49	42	-	-	-	-	-	-
<i>Senecio jacobaeae</i>	Asteraceae	19	47	-	-	-	-	-	-
<i>Cirsium vulgare</i>	Asteraceae	15	1	0	0	11	5	16	4
<i>Yellow composite</i>	Asteraceae	5	1	-	-	-	-	-	-
<i>Cirsium arvense</i>	Asteraceae	1	1	0	2	6	4	0	0
<i>Arctium lappa</i>	Asteraceae	-	-	0	0	4	<1	0	0
<i>Trifolium pratense</i>	Fabaceae	6	0	19	0	2	<1	8	0
<i>Trifolium repens</i>	Fabaceae	1	2	0	90	7	60	8	42
<i>Vicia cracca</i>	Fabaceae	<1	<1	0	0	0	0	0	0
<i>Vicia ervilia</i>	Fabaceae	-	-	44	2	0	0	0	0
<i>Anthyllis vulneraria</i>	Fabaceae	1	6	-	-	-	-	-	-
<i>Lathyrus pratensis</i>	Fabaceae	-	-	6	0	0	0	0	0
<i>Odontites verna</i>	Scrophulariaceae	2	<1	-	-	-	-	-	-
<i>Symphytum officinale</i>	Boraginaceae	-	-	25	2	4	0	4	0
<i>Rubus fruticosus</i>	Rosaceae	-	-	0	4	41	13	12	8
<i>Lamium album</i>	Lamiaceae	-	-	6	0	2	0	8	0
<i>Epilobium spp.</i>	Onagraceae	-	-	0	0	21	17	28	42
<i>Hypericum spp.</i>	Clusiaceae	-	-	0	0	2	0	0	0
<i>Dipsacus fullonum</i>	Dipsacaceae	-	-	0	0	0	<1	16	0
<i>Solanum dulcamara</i>	Solanaceae	-	-	0	0	0	0	0	4

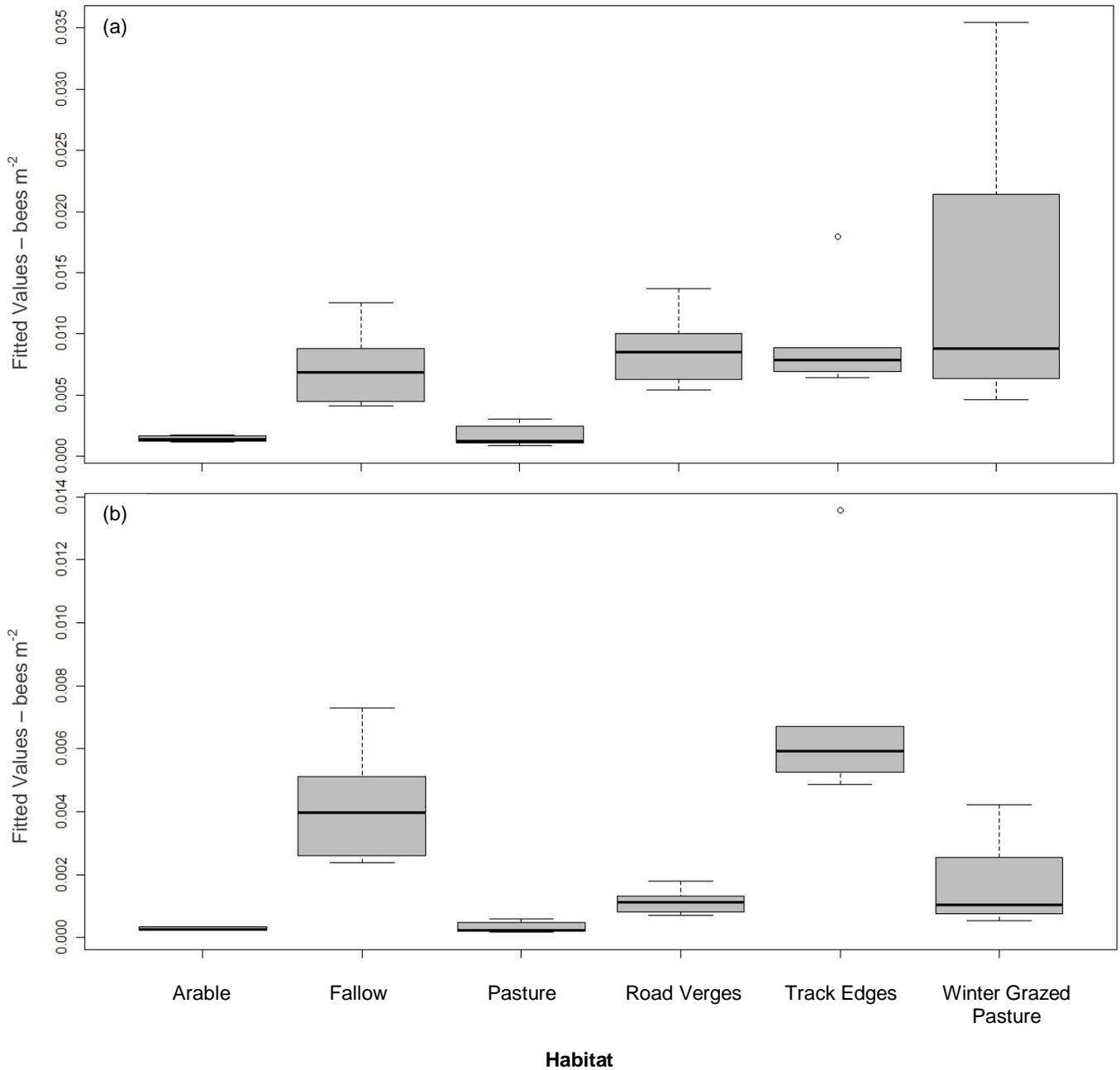
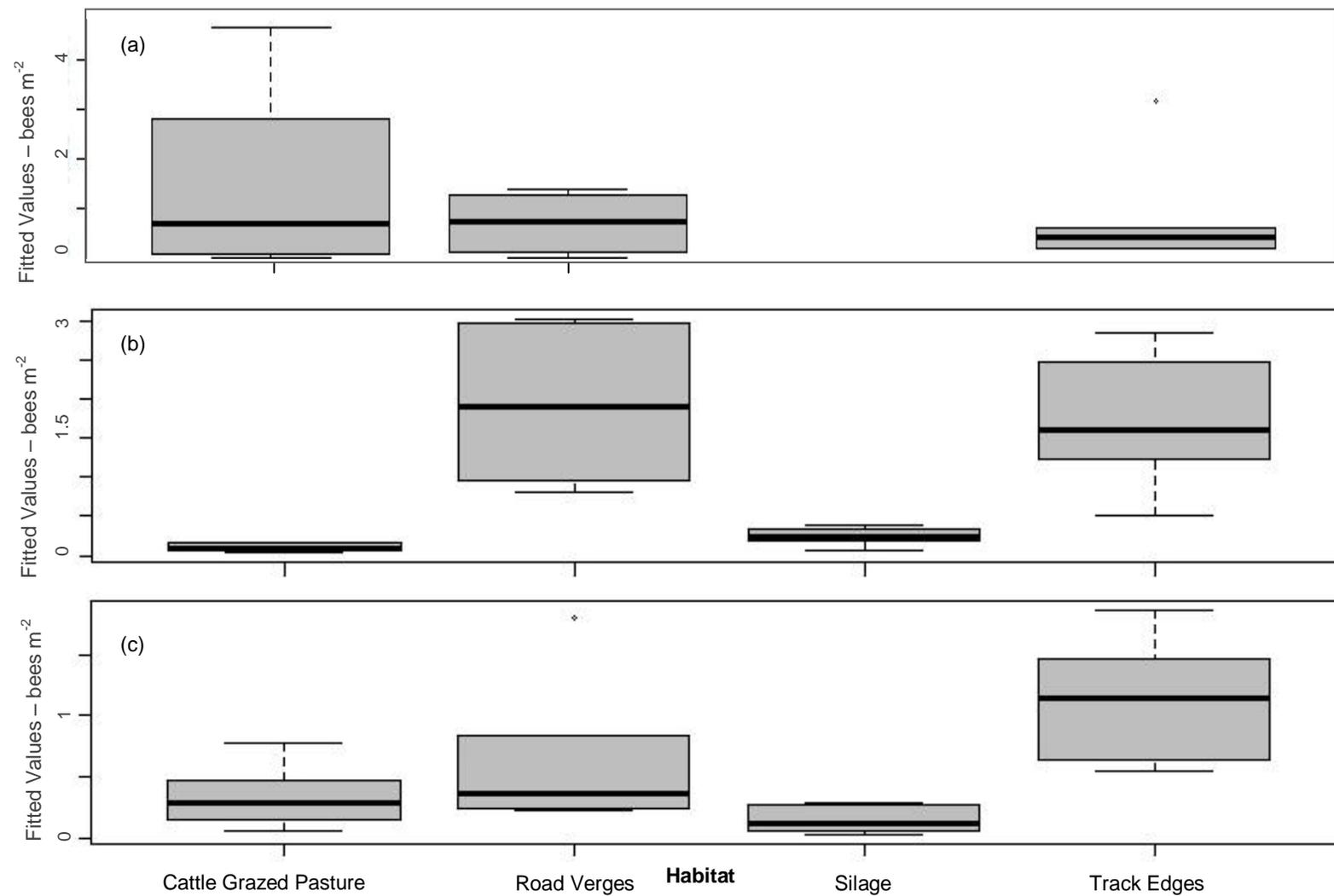
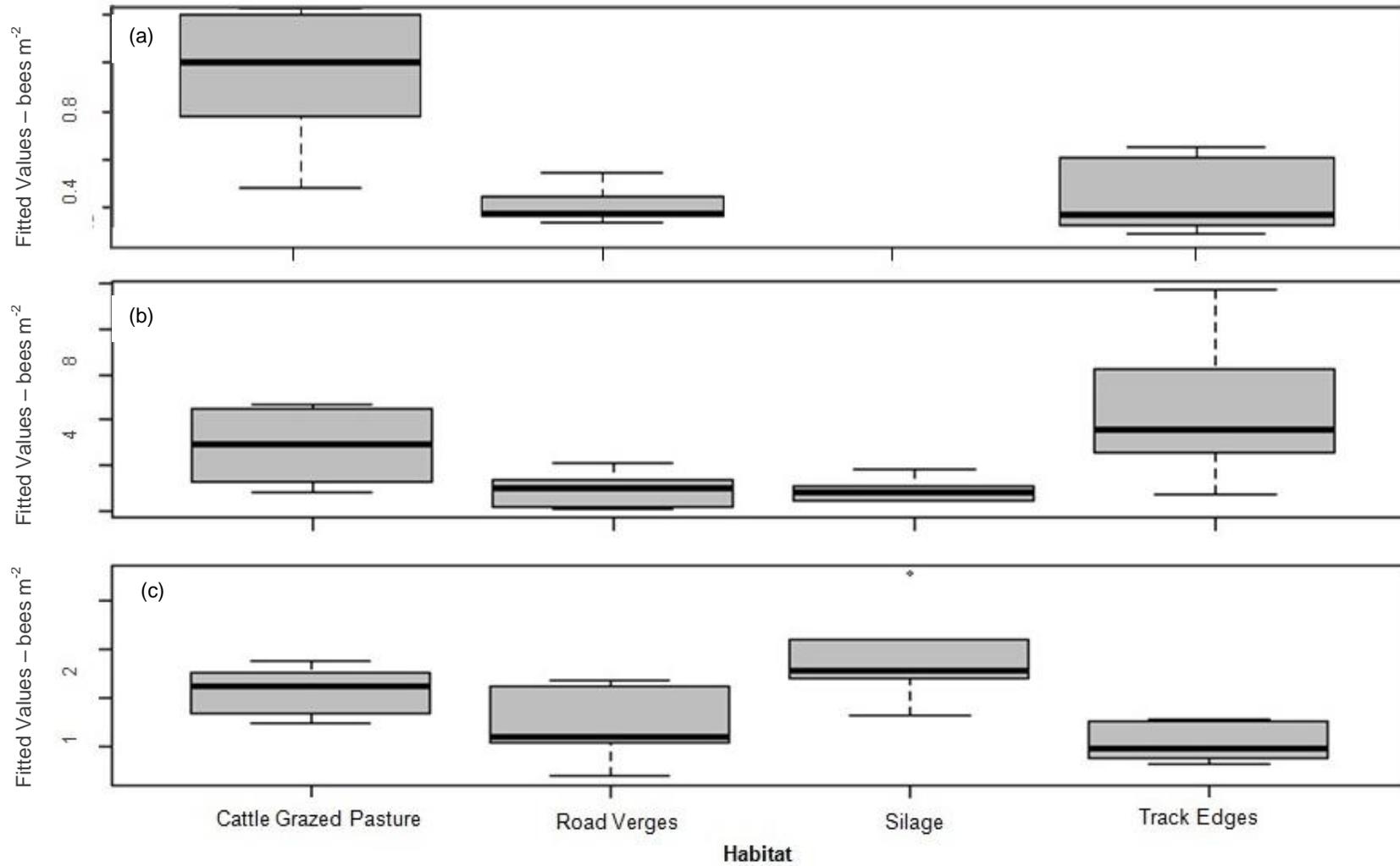


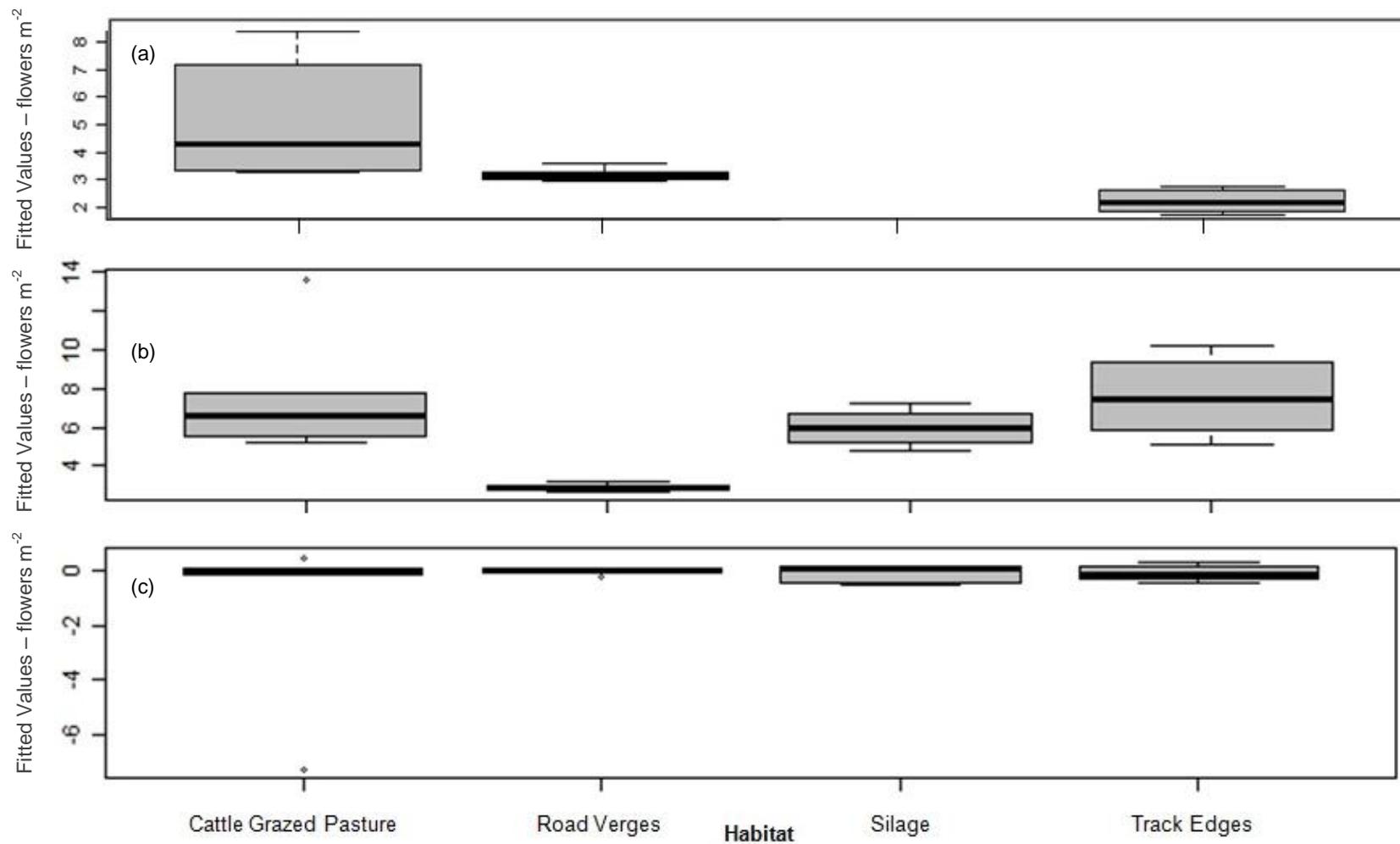
Fig. 3.1a-b. Box plots showing fitted values from the model for long-tongued bumblebee abundance (a) and the model for short-tongued bumblebee abundance (b) across six different habitats in the Outer Hebrides in 2009. Boxes represent the location of the middle 50 percent of the data and the whiskers indicate the interquartile range of the data.



Figs. 3.2a-c. Box plots showing fitted values from the models for long-tongued bumblebee abundance across four different habitats in the Somerset Levels. Boxes represent the location of the middle 50 percent of the data and the whiskers indicate the interquartile range of the data.



Figs. 3.3a-c. Box plots showing fitted values from the models for short-tongued bumblebee abundance across four different habitats in the Somerset Levels. Boxes represent the location of the middle 50 percent of the data and the whiskers indicate the interquartile range of the data



Figs. 3.4a-c. Box plots showing fitted values from the models for the abundance of bumblebee forage plants on four different habitats in the Somerset Levels. Boxes represent the location of the middle 50 percent of the data and the whiskers indicate the interquartile range of the data.

3.5. Discussion

3.5.1. *The effect of habitat on bumblebee abundance and the availability of key bumblebee forage plants*

Landscape heterogeneity has been shown to promote bumblebee abundance and diversity (Charman, 2007; Rundlöf *et al.*, 2008), as well as species richness for a range of other taxa, in agricultural landscapes (Weibull *et al.*, 2003). I found that both agricultural and adjacent non-agricultural habitats were utilised by foraging bumblebees in both study areas, but off-farm habitats were of greater importance to long-tongued species than the adjacent agricultural habitats. Similarly, Mänd *et al.* (2002) also found greater diversity of foraging bumblebees within non-agricultural habitats adjacent to farmland in Estonia. Track edges and road verges are outside the direct influence of farm management practices, although they are still subject to indirect influences from the adjacent agricultural land. Track edges are a typical feature of unfenced machair and are thus likely to be influenced by the presence or absence of grazing livestock. Similarly, on the Somerset Levels this habitat is frequently exposed to movements of livestock and is subject to some degree of grazing. Road verges would not intentionally be grazed at any time during the year; however, the movement of livestock, intermittent grazing by animals in adjacent fields, and vehicular disturbance relating to farming activities may have proved sufficient to generate the high levels of floral abundance, and therefore bumblebee abundance, observed on this habitat in crofted areas. High bumblebee abundances on track edges were also observed by Carvell (2002) on Salisbury Plain in the UK.

Crofting is currently undergoing agricultural intensification, with increases in sheep grazing on inbye land the most notable change. This practice was common throughout the Hebridean study area, and was highlighted in Chapter 2 as particularly detrimental to foraging bumblebees. Agricultural intensification on grassland habitats in this region is

driving the loss of forage plants from the landscape. Therefore non-agricultural habitats, such as road verges and track edges, are increasingly important for providing additional sources of forage, and may increase the abundance and diversity of bumblebee populations if managed correctly. For example, in Kansas, USA, Hopwood (2008) demonstrated that bumblebee species richness and abundance were significantly greater on road verges that had been restored to native vegetation rather than verges where non-native species dominated. While off-farm habitats also provided important foraging habitats for long-tongued species in both the Outer Hebrides and Somerset, in the latter region cattle grazed fields and silage provided an abundance of key forage plants for short-tongued bumblebee species. These management practices are employed by many farmers across the Somerset Levels, and create important foraging habitats for short-tongued species for a considerable proportion of the bumblebee's flight period. Properly managed grazing and cutting regimes may therefore benefit some bumblebees. Indeed, Carvell (2002) also identified cattle grazing as a beneficial management tool for promoting bumblebee abundance in grassland landscapes in southern England, and highlighted the importance of extensive cattle grazing between April and September. Although our results lend support to the use of this grazing regime, cattle grazing alone is probably not sufficient to maintain viable short-tongued bumblebee populations on the Somerset Levels. Bumblebee abundance fell dramatically in August, in line with a decline in forage plants. The availability and abundance of key bumblebee forage plants throughout the flight season are crucial for maintaining diverse bumblebee assemblages (Bäckman and Tiainen, 2002; Westphal *et al.*, 2006; Goulson *et al.*, 2008b), therefore additional sources of forage are required in late summer to support the final stages of colony development.

3.5.2. *Bumblebee floral resource use*

In accordance with previous studies (*e.g.* Goulson and Darvill, 2004; Redpath *et al.*, 2010), my data shows that bumblebees utilise a few key bumblebee forage plant species rather than particularly diverse floral assemblages. Of the 10 flowering plant species that bumblebees were recorded using in the Outer Hebrides, only three made up 85% of all foraging visits. *C. nigra* was the most frequented by long tongued bumblebees and its availability within the landscape was significantly related to the abundance of this group. *C. nigra* is known to be an important resource for both *B. distinguendus* and *B. muscorum* (Benton, 2006).

A large proportion of the bumblebees recorded on the Somerset Levels belonged to the short-tongued sub-group. Short-tongued bumblebees are more general in their dietary requirements than longer tongued species and exploit a wider range of floral resources (Goulson and Darvill, 2004; Goulson *et al.*, 2005), including non-native and cultivated flowers found in urban areas (Goulson *et al.*, 2002). *T. repens* was a particularly important source of forage for short-tongued bumblebees early in the season. This species was predominantly located on cattle grazed pasture and silage fields, therefore accounting for the strong association between short-tongued bumblebees and these farmland habitats.

3.5.3. *Implications for conservation management*

Both this study and that carried out in Chapter 2 highlight the negative impact on bumblebee populations of the increasingly intensive livestock production methods employed in the Outer Hebrides. Management of winter grazed pasture, where livestock are absent from lowland grassland areas for a period during the summer allowing the sward to regenerate, reflects historical grazing regimes. However, winter grazing is more commonly found on the machair grasslands than the lowland inbye areas which are

increasingly intensively grazed by sheep throughout the year (Willis, 1991; Sutherland and Bevan, 2001). My data demonstrate that summer grazed areas in this region have fewer flowers and bumblebees. In contrast, in the cattle grazing systems typical of lowland regions, grazing throughout the summer is an efficient means of providing forage for a lengthy period during the early-mid flight period. However, additional forage is required in these landscapes later in the season to support the final stages of colony development of both long- and short-tongued bumblebees. This may come from non-agricultural habitats, such as track edges and road verges, or may require the introduction of additional management practices, such as the introduction of a wildflower seed mix, that would fill this resource gap.

The rural road network may provide important habitats for farmland biodiversity (Pauwels and Gulinck, 2000), and road verges have previously been shown to be valuable habitats for bumblebees (Hopwood, 2008). These habitats also have the potential to be managed for the benefit of a range of other insects (*e.g.* Saarinen *et al.*, 2005; Noordijk *et al.*, 2009). The results of this study suggest that road verges and track edges are of greater value to long-tongued bumblebees, particularly in intensively managed agricultural landscapes.

3.5.4. *Conclusions*

The value of non-agricultural habitats to foraging bumblebees in farmed landscapes varies in relation to the intensity of the farming practices utilised on the adjacent farmland and with the type of bumblebee species – either long- or short-tongued. The value of track edges and road verges to long-tongued bumblebees is likely to be applicable to other regions, both within the UK and Europe, where intensive agriculture limits landscape heterogeneity and the availability of suitable forage material. The responsibility for the management of road verges falls to local authorities. Any management they implement

needs to be sympathetic to the requirements of bumblebees and other invertebrates that utilise these habitats, *i.e.* cutting regimes should ensure forage remains available throughout the season. As road verges are found on non-agricultural land they fall outside the scope of Agri-Environment Scheme (AES) payments to encourage beneficial management practices. Therefore, I suggest that road verges are integrated into local land management plans in areas characterised by intensive agricultural practices to ensure suitable management is maintained for bumblebees and other invertebrates throughout the year.

Grazing regimes are an important means of promoting floral abundance and diversity in both grassland farming systems we examined. However, this study indicates that a 'one size fits all' approach is not appropriate, with different grazing regimes required in different regions. In marginal, mixed livestock farming systems characteristic of the Outer Hebrides reducing summer grazing on inbye land by both cattle and sheep would be highly beneficial for bumblebee forage plants and therefore help support bumblebee populations. In contrast, extensive grazing throughout the summer provides a wealth of foraging resources for short-tongued bumblebees found in lowland grassland areas, such as the Somerset Levels and Salisbury Plain. Therefore the type and intensity of production of the farming system in use need to be taken into account in developing any grazing management prescriptions for AES which are aimed at providing bumblebee forage plants in agricultural grassland habitats.

Chapter 4. Ecological-Economic modelling: Using interdisciplinary models to conserve the natural environment

4.1. Abstract

The provision of ecosystem services, such as reduced soil erosion, often relies on human intervention and may provide direct and indirect economic benefits. Consequently, the resulting close relationships that exist between the two disciplines of ecology and economics means that both ecological and socio-economic factors should be taken into consideration when examining questions relating to conservation and the provision of ecosystem services. Ecological-economic modelling provides an interdisciplinary approach to addressing socio-ecological questions; however, differences in approaches and technical terminology associated with both disciplines, coupled with a lack of knowledge can limit the opportunities for collaborative research. Here I review the applications of ecological-economic models to environmental questions, and focus on two commonly used modelling frameworks: mathematical modelling using linear programming and simulation using agent-based models. This review provides examples of where these two approaches have been utilised and highlights the scope of interdisciplinary research for conserving the natural environment.

4.2. Introduction

Interdisciplinary research incorporating aspects of both the social and environmental sciences to address questions relating to conservation and the provision of ecosystem services is not a new concept, with examples of studies combining economics with ecological data dating back to the late 1990s (*e.g.* Hanley *et al.*, 1996; Ando *et al.*, 1998; Tucker *et al.*, 1998). Although the use of ecological-economic models is evident in studies throughout the past decade, the widespread uptake of this approach to socio-ecological

research has been slow, despite acknowledgement from both the social and environmental sciences that this approach can be beneficial (Mascia *et al.*, 2003; Lawton, 2007). The bias of research institutions to single subject research and the attitudes of researchers towards colleagues in other disciplines have previously been identified as prohibitive factors in the development of interdisciplinary research and may help explain this slow uptake (Wätzold *et al.*, 2006). The attitudes of researchers have received particular attention from Wätzold *et al.* (2006) who suggest that the different ways in which ecologists and economists approach a problem, and the associated technical terminology, can limit opportunities for collaboration. In addition, many researchers may be unaware of the benefits derived from incorporating data from other disciplines (Wätzold *et al.*, 2006). For example, biodiversity conservation and the provision of ecosystem services to wider society invariably depend on some form of human intervention and often provide direct and indirect economic benefits, therefore creating relationships between the two disciplines and generating opportunity costs, in terms of alternate land-uses, *etc.* Consequently, both ecological and socio-economic factors should be taken into consideration within the same modelling framework to ensure a good depiction of the study system and the inclusion of trade-offs between environmental and socio-economic requirements. Although many environmental problems can be analysed using a single disciplinary approach, each process often results in a different outcome depending on the objective of the method used. Therefore, employing an interdisciplinary approach to socio-ecological problems may highlight important outcomes that might not otherwise be identified by single discipline models (Cooke *et al.*, 2009). This is particularly relevant to biodiversity management where ecological and socio-economic factors impact on the persistence of a species or the preservation of a particular habitat. Without employing an integrated approach, we cannot model or fully comprehend the economic pressures which influence these threats.

The scope of interdisciplinary research utilising ecological-economic modelling techniques is vast, with studies ranging from preserving ecosystem services and enabling sustainable development of rural communities in developing countries (*e.g.* Carpentier *et al.*, 2000; Dogliotti *et al.*, 2005) to creating cost-efficient agricultural payment schemes to conserve farmland biodiversity in Europe (*e.g.* Drechsler *et al.*, 2007b). However, several challenges to this type of collaborative research have been identified (Wätzold *et al.*, 2006). The need for an in-depth knowledge of both subject areas is important but difficult to achieve with different mindsets, terminology and approaches. Cooke *et al.* (2009) have gone some way to address this issue by providing ecologists with a guide to the quantitative methods used by social scientists and an overview of the terminology used, thus opening up the field of environmental economics to a wider audience. Similarly, the way in which ecologists and economists design their studies, choose their research questions and the spatio-temporal scales they examine can be difficult to reconcile. Again, recent reviews such as Eppink and van den Bergh (2007) and Cooke *et al.* (2009) tackle this issue by evaluating methods and providing guidance on the most appropriate to use depending on the research question, thus making both subject areas more accessible and comprehensible. The final challenge suggested by Wätzold *et al.* (2006) relates specifically to modelling. Models are used by both ecologists and economists; however, ecological models tend to be complex and targeted, such as focusing on a single species (Wätzold *et al.*, 2006). In contrast, economic models are often less complex and more general, addressing more conceptual ideas (Drechsler *et al.*, 2005). Differences in spatio-temporal scales are also apparent, with economic models often not considering uncertainty (Drechsler *et al.*, 2005), whilst ecological models tend to examine specific geographic regions or time periods, and take into account ecological uncertainty (Wätzold *et al.*, 2006). Although these challenges represent significant obstacles to interdisciplinary research, the uptake of this type of modelling framework is now becoming more frequent

throughout the academic world, as demonstrated by the proportion of papers cited here that utilise ecological-economic modelling and have been published since Wätzold *et al.* (2006).

In this chapter I aim to help address the second barrier to interdisciplinary research identified by Wätzold *et al.* (2006) (*i.e.* the mindset of researchers) by highlighting the versatility of ecological-economic models. In Section 2 I discuss the general application of interdisciplinary models to demonstrate the diverse array of topics that these methods may be applied to, and in Section 3 I discuss in greater detail the application of two types of ecological-economic modelling frameworks: mathematical programming models and agent-based models.

4.3. Applications of ecological-economic models

The integration of ecological and economic data enables a diverse array of environmental issues to be addressed. The principal benefit of this combined interdisciplinary approach is that the modelling framework enables the complex nature of the interactions between the natural world and anthropogenic factors, such as socio-cultural and economic issues, to be taken into consideration. Models can be utilised to predict human behaviour and the associated environmental or ecological effects, or to assess the consequences of ecological change on human welfare (Cooke *et al.*, 2009). Several modelling approaches have been identified as most suitable for ecologists to predict behaviour (Cooke *et al.*, 2009). These include: optimisation, in which humans are assumed to behave as rational optimising agents; and, predicting behaviour from an agent's motivations. From an economist's viewpoint, four types of model are often used to examine combined environmental and social issues: general equilibrium, macroeconomic growth, cost-effectiveness, and renewable resource extraction models (Eppink and van den Bergh, 2007). In terms of

biodiversity conservation, general equilibrium and macro-economic growth models are rarely used, and the attention to ecological detail tends to decline in line with increasing complexity of the economic model (Eppink and van den Bergh, 2007). Cost-effectiveness models are the most frequently utilised, and can be applied to questions involving conservation or resource management under budgetary constraints. These models deal with efficient allocation of funds in situations of habitat loss and degradation where targets are set. They are also useful in calculating the production possibility frontier (PPF), which provides information on the levels of environmental and economic variables required to achieve the desired environmental outcome with no loss to either variable (Eppink and van den Bergh, 2007). Consequently, these models feature heavily in this review. Renewable resource extraction models are applicable to natural resources that gain an economic value when harvested, such as fisheries, and examine issues relating to individual and socially optimal resource harvesting rates and different property rights (Eppink and van den Bergh, 2007).

The ecological elements of interdisciplinary models are often derived from separate ecological sub-models, with some form of ecological link function incorporated into the final model to integrate the ecological and economic datasets. This can be achieved by including ecological data as a set of coefficients within the input-output matrix of mathematical programming models (*e.g.* Pacini *et al.*, 2004a), or through the inclusion of constraints within the final model to link profit-maximising behaviour to land-use and, in turn, relate these to possible ecological consequences (*e.g.* Nalle *et al.*, 2004; Drechsler *et al.*, 2007b).

In this section I provide an overview of the broad range of topics that interdisciplinary models can be applied to in order to illustrate the diversity of problems that ecologists, and economists, can explore using this type of integrated approach.

4.3.1. The development of cost-effective conservation payments

The application of ecological-economic models is helpful in examining the development of cost-effective payments for environmental services, and such models are also particularly useful for examining future changes to agri-environmental policies and market conditions. Payments to encourage land managers to voluntarily undertake ecologically beneficial land management are the principal mechanisms used in the US and EU to deliver environmental services on private land. In the EU, the primary mechanism for member states to promote the provision of environmental services by farmers and land-managers is through Agri-Environmental Schemes (AES), whereby farmers are compensated for utilising ecologically sound agricultural practices. However, payments are often uniform, both spatially and temporally, and therefore do not take into consideration the mobility of organisms, the spatio-temporal variation in resource availability or variation in the private costs of supplying these environmental services. Uniformity of payments may also lead to the over-compensation of some farmers due to varying implementation costs incurred by individuals participating in a scheme. The converse is also true. In addition, the differing attitudes of farmers towards conservation may also result in different levels of compensation payments being sought. These factors all contribute to the inefficient allocation of conservation funds. Consequently, ecological-economic models have an important role in allowing the ecological complexities of species and habitat conservation, and the impacts of policy or markets changes, to be examined in conjunction with the economic costs of implementing conservation measures. Therefore, this enables a cost-effective approach to payments to be developed, and is highlighted by Drechsler *et al.*

(2007b) who undertake ecological-economic modelling to develop a cost-effective payment scheme for the conservation of the large blue butterfly, *Maculinea teleius*. In this instance, metapopulation dynamics of the butterfly are integrated into the modelling framework. The utilisation of an interdisciplinary model also enabled the authors to compare homogeneous and heterogeneous payment schemes. Their results show that the latter payment scheme provides greater environmental gains for a given budget and demonstrates the importance of heterogeneous conservation policies. However, their case study does highlight the difficulty of creating spatially-heterogeneous payment schemes, as the ecological benefit is dependent on the presence of other land parcels subject to the same management regime located nearby. This requirement to link fragmented habitats together (*i.e.* ecological connectivity) within the agricultural landscape is an important aspect of biodiversity conservation that can also be addressed with the aid of ecological-economic models. For example, Drechsler *et al.* (2007a) developed a modelling framework to design payments to promote spatio-temporal landscape heterogeneity to conserve three grassland species whilst, more recently, Drechsler *et al.* (2010) consider the cost-effectiveness of an agglomeration bonus (an additional payment received when management is undertaken to produce an ecologically beneficial spatial arrangement of habitats within the landscape) in comparison to a homogeneous payment system.

4.3.2. *Land-use planning*

Agricultural intensification has been identified as the primary driver behind declines in farmland biodiversity throughout the EU during the latter half of the twentieth century (Chamberlain *et al.*, 2000; Robinson and Sutherland, 2002). In many cases rare species are associated with traditional farming practises that have now been replaced by more efficient and intensive methods, *e.g.* haymaking has been superseded by silage production throughout much of the UK. In addition, traditional agricultural practices are often closely

linked with rural cultures. For example, traditional farming practices in the Mediterranean are influenced by cultural and social factors, as well as environmental factors, which has led to a stable equilibrium being achieved between agriculture and the environment (de Aranzabal *et al.*, 2008). However, changing socio-cultural conditions have led to a shift in land management practices, resulting in negative environmental impacts, such as soil erosion and habitat loss (de Aranzabal *et al.*, 2008). This is also apparent within crofting communities in the north of Scotland (Chapter 2). Consequently, conservation and farming are often in opposition to one another, especially as the necessary land management changes required to meet conservation targets create opportunity costs which are incurred by the land manager or farmer. Ecological-economic models provide a useful planning tool which can help the user examine the opportunity costs of changing land management practises by private land managers, and also the likely ecological impacts. For example, House *et al.* (2008) applied this method to examine the potential for improving conservation on three mixed cropping-livestock farms in eastern Australia. Increasing conservation effort through increasing tree and shrub cover reduces the area of land that can be under agricultural management, therefore creating a trade-off between farming and conservation. In this instance, model simulations were able to show that relatively small changes in farm management could have significant effects on net profits or losses for the farmer. The results of this study illustrate that economic uncertainty relating to farm income acts as a barrier to farmers voluntarily implementing environmentally sensitive measures in Australia, and clearly shows how studies utilising interdisciplinary methods can provide guidance for land-use planners and policy makers in general. Similarly, Dorrough *et al.* (2008) show that ecological uncertainty may also influence an individual's land management decisions, and therefore the strategies required by land-use planners to achieve desired environmental outcomes. In this study, the integrated modelling approach enabled the authors to highlight the different opportunity

costs associated with two conservation strategies for regenerating tree cover on farms in Australia. The results of the study provide planners with information on the likely responses of farmers to each conservation strategy, and subsequently aid policy design. Further studies have also used interdisciplinary methods to examine the impacts of policy and sustainability at the farm level (e.g. Münier *et al.*, 2004; Meyer-Aurich, 2005). Model simulations of land-use changes in rural landscapes of the Mediterranean in response to socio-economic scenarios also present the case for an integrated modelling approach to environmental issues and the development of conservation and sustainable development policy (de Aranzabal *et al.*, 2008).

Land-use planners may also benefit from the use of ecological-economic models in situations other than agricultural systems. The balance between conservation and other land-uses is delicate and, as with agriculture, management practices that promote biodiversity do not always promote the optimal land-use for commercial or development activities. For example, combined modelling techniques incorporating social welfare indicators have demonstrated that wetland conservation and urban growth and development are not compatible, with biodiversity suffering in response to urban expansion, and urban and economic growth becoming limited if a greater value is placed on conservation of the ecological resource (Eppink *et al.*, 2004). However, biodiversity and other land-uses are not always in conflict. By simulating a series of current land-uses in comparison to cost-effective alternative scenarios Nalle *et al.* (2004) determined that both ecological and economic gains could be achieved by modifying current practices used in timber production. Similarly, through the use of an interdisciplinary modelling approach, Polasky *et al.* (2005) also show that the trade-off between biodiversity and economics is not always negative, and that the efficient allocation of land for forestry,

agriculture and biodiversity could promote both economic and ecological benefits in the Willamette Basin, Oregon.

4.4. Mathematical programming and agent based models for ecological-economic modelling

There are a range of different ecological-economic modelling techniques available to apply to environmental issues (*e.g.* Cooke *et al.*, 2009). In this section I look in more detail at two types of modelling approach: optimisation using mathematical programming models and, agent based models.

4.4.1. Mathematical programming models

4.4.1.1. Linear Programming

Linear programming (LP) is a mathematical modelling technique that uses optimisation to either maximise or minimise a specific objective function, such as income.

The general structure of a LP model is:

Maximise ($Z = c'x$)

Subject to $Ax \leq b$

And $x \geq 0$

Where Z is the objective function (*e.g.* income net of variable costs) at the unit level (*e.g.* farm); x is the vector of activities; c is the net benefit per unit of activity; A is a matrix of input use coefficients; and, b is the vector of resource endowments or technical constraints (Hazell and Norton, 1986). In achieving the objective function, LP models determine the optimal solution for the allocation of limited or fixed resources, such as land. However, these models have several limitations, such as the assumption that all agents are rational

and exhibit optimising behaviour, and the linearity of constraints. Despite this, LP models provide a means of examining micro-level changes in agent behaviour in response to different scenarios across a range of systems, *e.g.* changes in farmer behaviour in response to agricultural policy changes across a range of farm types (Acs *et al.*, 2010). The marginal value product, or shadow price, of fully utilised resources is also calculated within the models (Barnard and Nix, 1979; Hazell and Norton, 1986). These additional data represent the trade-offs between different activities within the model and may be useful in informing further management or policy decisions, such as in the design of AES. To be able to base such decisions on the outputs of these simulations, models need to provide a good representation of the systems they are simulating. Consequently, calibration against a base year or an average over several years is required to ensure no large discrepancies exist between the model and the baseline (Howitt, 1995).

4.4.1.2. Positive mathematical programming

Positive Mathematical Programming (PMP) provides an alternative modelling system to the traditional LP model, by allowing the user to calibrate agricultural mathematical programming models to observed behaviour during a specified reference period (Howitt, 1995). Developed for instances when little information is available or where empirical constraints do not reproduce the reference period results (Howitt, 1995), and to take into consideration the heterogeneous nature of farming (Howitt, 1995; de Frahan *et al.*, 2007), PMP models provide the user with a more flexible modelling approach than LP (Howitt, 1995; de Frahan *et al.*, 2007), and form a link between programming and econometric models in agricultural economics (Heckelei and Britz, 2005).

PMP models aim to provide exact calibration to primary resource use (*i.e.* land, production and price; Howitt, 1995), and assume that observed levels of production are derived from

profit maximising behaviour (Schmid and Sinabell, 2005). This method calibrates models to observed data using the information provided by dual variable calibration constraints in a three step process, in which the duals are used to calibrate a non-linear objective function which, in turn, reproduces observed behaviour for the reference period without the need for calibration constraints (Howitt, 1995; de Frahan *et al.*, 2007). The term ‘positive’ refers to the parameters of the non-linear objective function and implies that these parameters are derived from rational behaviour when all observed and non-observed conditions producing the observed behaviour are considered, as in econometrics (de Frahan *et al.*, 2007). Unlike econometrics, PMP does not require observations to determine economic behaviour, although this prevents PMP from being applied to inference and validation tests (de Frahan *et al.*, 2007).

The three key steps in PMP are summarised below (Howitt, 1995; Heckeley and Britz, 2005; de Frahan *et al.*, 2007):

1. Within a mathematical programming model add a set of calibration constraints that bound activities to observed behaviour in the reference period to the limiting resource constraints.
2. Use dual variables to calibrate the parameters of the non-linear objective function.
3. Use the calibrated non-linear objective function in a non-linear programming problem similar to the original so that the observed activity levels are reproduced in the optimal model solution.

The main advantages of PMP models lie in their ability to calibrate to observed activities with few data and without the introduction of artificial constraints (Heckeley and Britz,

2005; de Frahan *et al.*, 2007). In addition, the use of non-linear terms in the model structure helps overcome the specialisation problems often experienced in LP, whilst the smoothness of responses to policy changes and other exogenous shocks is more realistic simulation behaviour (Heckelei and Britz, 2005; de Frahan *et al.*, 2007). However, despite increasing popularity, PMP remains a developing modelling system and has its limitations. For example, models only makes use of a single data point, disregarding pooled data or times series data, therefore only one observation for a farm is insufficient to estimate how it may respond to changing economic conditions (Heckelei and Britz, 2005; de Frahan *et al.*, 2007). The extension of these models to include risk, behavioural and environmental parameters also needs to be taken into consideration to broaden the scope of their application (de Frahan *et al.*, 2007).

4.4.1.3. Linear programming and the provision of environmental services

The ability of LP models to determine the optimal levels of resource use makes them a valuable tool in farm planning (*e.g.* Faris and McPherson, 1957; Barnard and Nix, 1979; Cain *et al.*, 2007; Minh *et al.*, 2007). In addition, because they operate at the level of the individual agent this type of model lends itself to simulating the effects of changing agricultural policy on farmer behaviour (*e.g.* Pacini *et al.*, 2004a). Ecological and environmental data may also be incorporated, and these ecological-economic models may be used to examine a variety of issues, such as the trade-offs between agricultural sustainability and environmental outcomes (*e.g.* Pacini *et al.*, 2004b). Integrating ecology and economics in this way provides a useful tool for environmental managers trying to balance environmental services with the requirements of land users. For instance, Dogliotti *et al.* (2005) use mixed integer LP models to examine the sustainable development of small-scale vegetable farmers in the Canelo'n Grande region of Uruguay. Here, model outputs suggest that modifying current farming practices provides

opportunities for farmers to increase their income whilst reducing soil erosion and improving soil fertility. Similarly, Kaur *et al.* (2004) use LP models to determine optimal land use plans within a watershed to minimise soil erosion. Optimisation techniques have also been used to highlight the negative trade-offs between socio-economic and environmental sustainability relating to agricultural and water policy scenarios for a range of irrigated farming systems in Italy (Bartolini *et al.*, 2007). LP models can also be applied to a wide range of environmental and socio-economic questions beyond those posed by agricultural systems; Hastings *et al.* (2006), and Hall and Hastings (2007) use this method to determine optimal strategies for controlling invasive species in the US, whilst Tucker *et al.* (1998) use cost minimisation techniques to restore habitats damaged by human activity on army training bases subject to budgetary constraints. These ecological-economic models may also be applied at different scales, with studies focusing on behavioural responses of farmers to agricultural policies examined at the farm level (*e.g.* Pacini *et al.*, 2004b; Acs *et al.*, 2010), whilst models addressing rural development may be at a regional scale (*e.g.* Hengsdijk *et al.*, 2007).

4.4.1.4. Linear programming and biodiversity conservation

In addition to the provision of environmental services, such as reduced soil erosion, optimisation using LP models can be applied to species and habitat conservation issues. Threats to biodiversity often occur as a direct result of anthropogenic pressures on the environment, such as deforestation to increase timber production or to aid the development of rural communities. Consequently, there is a trade-off between the need for conservation and the socio-economic requirements of society. The opportunity costs of changing land-use form the basis of these trade-offs, and LP models are particularly useful in examining this relationship as they enable a range of scenarios over several different systems (*e.g.* land-uses, farm types) to be investigated. For example, using this method Tyynelä *et al.*

(2003) were able to predict the impacts of three different land-use scenarios on rural communities and tree species richness as part of a forestry plantation scheme in Indonesia, whilst Carpentier *et al.* (2000) were able to simulate four types of agricultural intensification scenarios to investigate whether farmers in the western Brazilian Amazon would take up more intensive practices, and predict the likely impacts on farm income and deforestation. This feature may also be used by ecologists to compare levels of biodiversity in different areas or habitats. For example, Perhans *et al.* (2007) utilised a LP based method of site selection to compare how efficient four different forest types were at capturing biodiversity. LP models are also extremely useful for ecologists looking to allocate land for conservation in the most cost-effective manner whilst allowing sustainable development for the benefit of society. This is demonstrated by Saldarriaga Isaza *et al.* (2007) in their study of huemul (*Hippocamelus bisulcus*) conservation in central Chile. By taking into consideration the habitat requirements of the target species they were able to show that current land management practices are not cost-effective and introducing alternative management strategies would be of both ecological and economic benefit. In addition, this type of modelling framework is also useful for land-managers trying to balance conservation with commercial production. For example, MacMillan and Marshall (2004) use LP models to develop short-term timber harvesting programmes to help forestry managers maximise the quality of capercaillie (*Tetrao urogallus*) habitat in Scotland. LP models also provide a valuable tool for planners and policy-makers when making decisions relating to optimal land acquisitions under budgetary constraints (*e.g.* Messer, 2006), or in determining the payment rates required to encourage farmers to implement environmentally beneficial management practices to aid conservation (*e.g.* Hanley *et al.*, 1998). In the latter instance, the marginal value product generated in the model output is particularly useful as it calculates the cost associated with tightening a constraint by one extra unit, *i.e.* it provides a measure of the financial cost associated with

increasing biodiversity, and can indicate the level of incentive required to generate the desired environmental outcome.

4.4.2. *Agent-based modelling*

Agent-based models (ABM) form a relatively new modelling framework that enables the user to model complex systems and simulate the behavioural responses of autonomous agents to their environment (Macal and North, 2010). A bottom-up approach, ABM provides a means of modelling the interactions between individual agents with other agents and their environment, and has the capacity for agents to influence and learn from each other, and modify their behaviour so that they become better adapted to their environment (Macal and North, 2010). The inclusion of agent interactions in the model is a particularly useful method for modelling aspects of social behaviour, whilst modelling agents at the individual level allows the user to incorporate the complexities of the relationships that exist between agents and generates the behaviour of the modelling system (Macal and North, 2010). This ability of ABM to explore macro-level responses to micro-level changes in the behaviour of diverse agents interacting within a specific environment (Heckbert *et al.*, 2010), means that ABM are often considered to be both more flexible in comparison to mathematical models (*e.g.* LP models), which assume agents to be homogenous and exhibit rational behaviour, and are more accurate than a description of the system under investigation.

The general structure of an ABM typically consists of three elements: agents; the relationships of the agents and the methods of agent interaction; and, the agent's environment (Macal and North, 2010). Agents are autonomous (*i.e.* act independently), display heterogeneous characteristics and are self-contained. They are often active and able to interact with other agents, either directly or indirectly. As social entities, agents

have dynamic interactions with one another that can influence their behaviour (Macal and North, 2010). Agents have the capacity to learn and adapt to their environment, but decisions are often made on the basis of incomplete information, therefore agents are assumed to act as boundedly rational entities (Heckbert *et al.*, 2010). Agents may represent individuals, such as farmers, or businesses, communities or even countries. The environment within which the agents act may represent a real geographic area or a social network, and provides agents with resources (*e.g.* energy, information) and a medium through which information can travel.

As with mathematical programming models, model validation is required to ensure the model is representative of the system it is simulating. However, for models that represent macro-level behavioural changes, it is difficult to identify whether the micro-level interactions that generate overall system behaviour are representative of the real world (Heckbert, 2009). In the absence of recognised model validation methods, modellers have started to develop empirical techniques to calibrate and validate ABM (Brooks and Shi, 2006; Heckbert, 2009). Empirical data may be gathered in many ways, such as socio-economic surveys, laboratory experiments or by using the historical output from a real system (Brooks and Shi, 2006; Heckbert, 2009). Empirical data may then be used to generate parameter estimates that reflect the data and test whether the model is a good reflection of the system it is simulating (Brooks and Shi, 2006).

The scope of ABM is far-reaching, from applications in the social sciences to cellular biology (Macal and North, 2010). Environmental factors may also be incorporated, and these ecological-economic models can be applied to problems relating to the management of natural resources and land-use change (Heckbert *et al.*, 2010). Here I illustrate some of the subject areas that ecological-economic ABM can be applied to.

4.4.2.1. Agent-based models and the conservation of biodiversity and ecosystem services

Like LP models, ABM can be utilised to address problems relating to conservation and sustainable development. For example, Hartig and Drechsler (2009) use an economic ABM combined with an ecological model to explore the effectiveness of market based instruments for species conservation when spatial connectivity is considered within the model framework, whilst An *et al.* (2005) utilise this modelling framework to simulate the impact of rural communities harvesting fuel-wood on giant panda (*Ailuropoda melanoleuca*) populations in China. Similarly, Heckbert *et al.* (2009) examine the impacts of hunting access on biodiversity through the development of forestry roads using this modelling framework. Mathevet *et al.* (2003) also use ABM to examine land-use changes, specifically looking at the relationships between hunting, farming and wildfowl populations in the Camargue, an internationally important wetland for migratory birds in southern France. Hunting makes a considerable contribution to the economy of this region; however, generating a good income requires a change in land-use from agriculture to hunting marshes and requires the intensification of management practices, which is detrimental to the wetland environment. Agriculture is predominantly the cultivation of rice crops which provide habitats that are complementary to the natural habitats of overwintering wildfowl. Due to economic pressures many landowners convert their agricultural land to hunting marshes, thus reducing the availability of suitable habitats. Interestingly, hunting is also reliant on agriculture for the hydrological services it provides, thus making this a particularly complex system. By utilising a multi-agent based modelling framework Mathevet *et al.* (2003) were able to consider the complex interactions within this system, examine the likely effects of different land-use scenarios and consider the implications for the conservation of this ecologically important region.

Examining the ecological and social impacts of the decision making behaviour of agents is also explored by Guzy *et al.* (2008). In this instance, ABM were applied to look at the likely effects of urban expansion on two different land-uses and the preservation of ecosystem services within the Willamette River Basin, Oregon. Alternate futures for the landscape were modelled by simulating a series of different policy scenarios, including agricultural and urban growth policies. The simulation results illustrate that encouraging farming and forestry activities, and containing urban expansion, could preserve ecosystem services in this region. Similarly, Schlüter and Pahl-Wostl (2007) employ a bottom-up modelling approach to the problem of socio-ecological resilience in a river basin system. By utilising an ABM framework, they were able examine the interactions of a community of agents within the river system, and determine the effects of both centralised and decentralised water allocation decisions on the sustainability of agriculture and the aquatic ecosystem.

In addition, ABMs provide a useful method of modelling social networks and can be applied to problems of sustainable development in rural areas, particularly in the developing world. For example, Schreinemachers *et al.* (2007) use an ABM approach that enabled the interactions between households to be modelled in order to investigate the relationships between soil fertility and rural poverty of two communities in Uganda.

4.5. Summary

The merits of integrating the disciplines of ecology and economics in the form of interdisciplinary models have been discussed at length by Wätzold *et al.* (2006). Here I show the variety of environmental issues that interdisciplinary models may be applied to. Ecological-economic models are particularly useful in land-use planning and aiding land managers to design optimal land-use allocations that increase land for biodiversity

conservation whilst ensuring land-managers remain with viable businesses. Models may also be applied to the conservation and preservation of other key environmental services, such as carbon sequestration or reducing soil erosion in vulnerable areas such as the Amazon, to explore ways of aiding the sustainable development of rural communities without further damaging or overexploiting natural resources. Although there are a range of different interdisciplinary methods available for ecological-economic modelling purposes, I have taken just two methods, mathematical programming and agent-based models, to highlight the diverse array of environmental and ecological problems to which these modelling frameworks can be applied. LP models operate at the micro-level, examining the small scale changes that occur in response to agent behaviour. Although these models require a lot of detailed information, the comprehensive nature of the models enables the minutiae of changes in resource allocation to be examined. This is particularly useful in farm planning for example, as the impacts of changes in agricultural policy are shown in changes in management at the farm-level. This application becomes more informative to conservation managers when ecological data are linked in, as users can test how different policies affect the availability of different land-uses and therefore make predictions about the abundance or persistence of the biodiversity associated with those land-use types. In both cases, this modelling framework is useful for informing policy-makers on the likely outcomes of future policies. LP models are limited in that not all agents behave in the same manner, therefore generalising from one farm does not mean that all farms will react to changes in the same way. In contrast, ABM look at the macro-level responses to micro-level changes, and so enable the user to predict the likely outcomes in the face of interacting agents who have different characteristics. This ability to look at interactions between agents with each other and their environment is useful for looking at a landscape scale, *e.g.* conserving biodiversity on privately owned agricultural land. Here ABM can look at how farmers communicate with each other and investigate

how the behaviour of one farmer influences the behaviour of another. They also enable the user to examine ecological connectivity and market-based payments, which are increasingly important aspects of agri-environmental payment design.

Chapter 5. Crofting and agricultural economics in the Outer Hebrides

5.1. Abstract

Crofting in the Outer Hebrides is a small scale form of agriculture which is unique to the Highlands and Islands of Scotland. Traditionally, crofting involved small scale livestock production and cultivation, with livestock moved to the moorland to graze during the summer months and cultivation on the machair (lowland grassland on sandy level plains behind the dune system). Cultivation and winter grazing on the machair promotes diverse wildflower assemblages, akin to the hay meadows once common across the mainland, and these habitats support important populations of endangered bumblebees. However, crofting is becoming more intensive in response to a range of socio-economic factors. Hay production has been replaced by silage and stocking densities of sheep have increased dramatically in the past 20 years. In addition, the age of active crofters is increasing and as a result livestock are rarely moved to the moorland in the summer, thus increasing the grazing pressure on the inbye and machair areas. These changes to crofting are threatening both the viability of crofting and the rare bumblebees that depend on the land crofters manage. In this study I show that in the Outer Hebrides crofting practices vary with island, with mixed livestock and arable production the primary activities on the Uists and Harris, whilst Lewis is generally limited to sheep production. The primary outputs are store livestock (either lambs or calves) on all the islands. On the Uists silage is grown to meet the feeding requirements of the livestock. Crofting on the Uists is the most profitable, although subsidies form a large proportion of their agricultural income. However, for many crofters agriculture does not form their main source of income, as in Lewis, where the majority of crofters worked on a part-time basis.

5.2. Introduction

Crofting is a unique form of agriculture that is characterised by small agricultural holdings clustered together in linear settlements, known as ‘townships’ (Stewart, 2005), and evolved following the Highland Clearances of the eighteenth and nineteenth centuries in northern Scotland (Willis, 1991). The agricultural units are called crofts after the Gaelic term ‘croit’ (which refers to a small area of enclosed land, Stewart 2005), and typically consist of enclosed areas of inbye land on which crofters rear both cattle and sheep, and undertake small scale rotational cropping activities. As members of the township, crofters have access to common grazings found on the moorland adjacent to the settlement (Stewart, 2005). Grazing clerks administer and regulate the allocation of common grazings for each township (Willis, 2001). Traditionally, these moorland areas were grazed by cattle and sheep throughout the summer, leaving lowland pastures to regenerate. Livestock were then moved down to the inbye during the winter months (Hance, 1952; Moisley, 1962; Caird, 1979; Stewart, 2005). In the Outer Hebrides, crofters also have shares of the machair, which are again held in common, and which provide suitable land for the majority of agricultural activities and is predominantly used for the cultivation of fodder crops (Hance, 1952; Caird, 1979). Historically, the use of artificial fertilizers was limited, with rotten seaweed and farm yard manure the primary methods of enhancing the nutrient poor soils. This combination of small scale agricultural operations and the limited use of artificial inputs created a method of farming which was environmentally sensitive and beneficial to biodiversity (Willis, 2001).

Crofting largely escaped the major impacts of agricultural intensification experienced elsewhere throughout the UK and western Europe during the latter half of the twentieth century and, as such, crofted landscapes now provide suitable habitats for some of the UK’s rarest biodiversity, notably the corncrake (*Crex crex*) and *B. distinguendus* (Love,

2003). However, crofting practices have evolved throughout this period and signs of intensification, and the subsequent impacts on biodiversity, are now evident (see Chapter 2). Increases in livestock production and output per hectare between 1970 – 1990 (Crofters Commission, 1991), the move from hay to silage production (Willis, 1991), and increases in sheep numbers and grazing of inbye land (Willis 1991), all point towards agricultural intensification. However, many of the observed changes in agricultural practices have arisen in response to the socio-economic changes taking place throughout the Crofting Counties. For example, the combination of rural depopulation and an increasing age structure throughout the region has led to a reduction in the number of crofters actively managing their land, increased the area of rush dominated (and therefore ecologically degraded) land (Crofters Commission, 1991), and perpetuated the trend for sheep production identified during the 1980s (Willis, 1991). Consequently, many older crofters now view crofting as a purely sheep based system (Willis, 2001). In addition, the number of crofting households fell by 23% throughout the Crofting Counties during the 1950s – 1980s (Crofters Commission, 1991), and now many crofters are responsible for the management of more than one croft, decreasing the mosaic of land-uses characteristic of traditional crofting and reducing the value of croft land to biodiversity.

Other socio-economic factors are also influencing crofting in the Outer Hebrides. The lack of skilled jobs in the region and the difficulty in finding affordable housing is driving the out-migration of younger age groups (Hall Aitken, 2007; Mackenzie, 2007), resulting in an increasingly elderly population (Hall Aitken, 2007; Comhairle nan Eilean Siar, 2009a,b). In contrast, the flow of people to the islands is characterised by middle class families looking for a better life in the Outer Hebrides (Willis, 2001), or foreign workers arriving to address labour shortages in non-agricultural industries (Hall Aitken, 2007). In addition, there is a trend towards living in more urban areas, particularly Stornoway (Hall Aitken,

2007). In addition, changes in agricultural subsidies and the Crofting Reform Act (2007) are influencing crofting. All these factors, in turn, impact on the number of active crofters and therefore how croft land is managed, although this has not been examined for the Outer Hebrides in any detail. Therefore, the aim of this chapter is to examine the range of socio-economic factors currently influencing crofter's land management decisions in the Outer Hebrides and to determine the economic state of crofting in this region. The results of the survey reported in this chapter are used to calibrate the ecological-economic mathematical models described in Chapter 6.

5.3. Methods

A croft survey was undertaken to establish which land management practices and production methods are currently employed by crofters in the Outer Hebrides, and to determine which socio-economic factors govern croft management decisions. The survey was based on that used by Acs *et al.* (2010) on upland farms in the Peak District, UK. Their study also aimed to gather socio-economic data from farmers relating to income and land management decisions to calibrate mathematical models, therefore the general structure of the survey was based on their work. Crofters in the Outer Hebrides were chosen from within the area studied in Chapter 2 to correspond with the survey of bumblebees utilising croft land in the region. This enabled data to be collected from a subsample of crofters who participated in both the ecological and economic surveys. An advert was placed in *The Crofter*, a magazine sent out to all members of the Scottish Crofting Foundation, to ask for volunteers and the contact details of possible participants were provided by staff belonging to organisations based within the study area (*e.g.* SNH, RSPB). Crofters were initially contacted by letter, followed by a telephone call. A total of 48 crofters were contacted across the study area and a positive response rate of 42% was achieved. 5% of completed surveys were unable to be included in any analyses, resulting

in a total sample size of n=19. Crofters from the islands of North and South Uist (n=9), Harris (n=3) and Lewis (n=7) were interviewed during site visits, except for a sub-group (16%) who completed the surveys themselves and returned them by post. All surveys were completed during the spring and summer of 2008. The survey focused on current management practices, the input and output costs associated with agricultural activity, and the subsidies received during the reference period (2007). A copy of the survey may be found in Appendix I.

5.4. Results

5.4.1. Croft history

All crofters in the survey undertook agricultural activities on their crofts during the reference period and have actively managed their land since the commencement of their tenancies. In general, crofters on the Uists and Harris have been actively involved in crofting for the longest period, with mean durations of 29 and 20 years (± 4 and 6 years respectively), compared to 14 years (± 5 years) on Lewis. This is unsurprising as 56% of Uist crofters and 67% of Harris crofters were estimated to be over the age of 60, compared to 14% on Lewis. Interestingly, no crofters under the age of 30 were recorded on the Uists, and the youngest age range recorded on Harris was 40-50. Lewis was the only island where all ages were represented and the most common age range did not fall in the over 60 category.

Multiple tenancies were a common feature of crofting in the Outer Hebrides, with 68% of all crofters responsible for the management of other crofts in addition to their own home croft. This feature was most common amongst crofters on the Uists and Lewis, with over 71% of crofters on both islands recorded to have multiple tenancies compared to 33% on Harris. In most instances crofters were responsible for the management of an additional

two crofts, although a small proportion of crofters managed a larger number of crofts, with 14% of crofters on Lewis responsible for an additional four crofts and 22% on the Uists managing an extra six crofts. Due to the high frequency of multiple tenancies in the survey all crofts under the management of a single crofter are considered as one enterprise and collectively referred to as the 'croft business'. The area of the croft business varied markedly between islands, with businesses on the Uists averaging 55 ha (not including shares in common moorland grazings). This equates to more than three times the area of croft businesses on Harris and is seven times greater than those on Lewis. Although crofters on the Uists and Harris had access to common grazings they were rarely made use of. The majority of crofters (78%) on Lewis had no access to common grazings and the few that did made no use of them.

5.4.2. Croft management

The management regimes implemented by crofters varied throughout the Outer Hebrides and two croft types were identified which correspond to the primary production methods utilised on each island. Mixed livestock production (sheep and beef) and arable activities were characteristic of the Uists and Harris, whilst sheep production was most common on Lewis (Table 5.1). Four land types were also identified: machair, semi-improved and improved grassland, and moorland (Table 5.2). Crofting practices on the Uists were generally on a larger scale than on the other islands, as suggested by the much greater mean croft business area. The system on Harris was similar although fewer livestock were produced and arable was not an important aspect of the system. Crofting on Lewis was quite different to the other islands in the study area; generally, crofts were much smaller, held fewer livestock and crofting was only a part-time activity.

Table 5.1. The primary production activities undertaken by crofters on each island in the study area.

Island	Characteristics
The Uists & Harris	Store lamb and store calve production with grass and arable silage production. Grass primarily cultivated on the improved inbye, arable silage cultivated on the machair. Cultivation and fallow periods on a two years cropped, two years fallow rotation. Arable production was less common and extensive on Harris.
Lewis	Store lamb production on the inbye. No arable production and no access to moorland grazings.

Table 5.2. The characteristics of the four main land-uses found throughout the study area.

Land Use Type	Characteristics
Machair	Lowland grassland areas adjacent to the coast formed from wind-blown shell sand. Sandy soils are low in nutrients and support a diverse variety of wildflowers. Land primarily used for the cultivation of arable silage and grazing
Semi-improved grassland	Inbye grassland which forms the main grazings for livestock. Inorganic fertilizers and farm yard manure applied infrequently. Land also used in the production of grass silage
Improved grassland	Inbye grassland regularly enhanced with inorganic fertilizers and used for grass silage production
Moorland	Unfenced heather moorland, often held in common

The primary production activities on mixed crofts were store lamb and store cattle production, with livestock sold at local markets (Lochmaddy, Lochboisdale and Stornoway). The scale of livestock production varied between the Uists and Harris, with greater livestock numbers produced on the Uists (Table 5.3). Despite these differences in scale a bias towards sheep production was observed across all mixed livestock crofts and is exemplified by an average sheep:cattle ratio of 5:1 on the Uists and 3:1 on Harris. North Country Cheviots and Blackface were the most frequently reared sheep breeds on this croft type. Highland cattle were rarely produced with crofters preferring more commercial cattle breeds, particularly Simmental, Limousin and Charolais. Fodder purchased from the

mainland generated the greatest variable costs for this croft type, accounting for 43% and 51% of sheep production costs, and 44% and 62% of cattle variable costs on the Uists and Harris respectively. The production of silage crops was the only arable activity on mixed crofts and was restricted to Uists crofts. This activity accounted for 37% of the variable costs generated by cattle production. A mixture of crops, typically a traditional combination of barley, oats and rye, were the most frequently cultivated form of arable silage. Cultivation was limited to shares of the machair, and followed a cropping regime of two years cropped followed by two years left fallow. Grass crops were also cultivated, although less frequently and only on improved inbye land. Artificial fertilizers (NPK) were applied to crops on both the machair (320 kg ha⁻¹) and inbye (348 kg ha⁻¹). Farm yard manure was added to fields as a by-product of grazing and in some instances crofters utilised rotten seaweed as a natural fertilizer. Only one cut of silage was taken from the machair and inbye in late summer, usually between August and September, and the mean yield of arable silage recorded during the reference period was 11.7 t ha⁻¹ (± 1.9 t ha⁻¹). The timing of the cut depended on whether the land was included in any agri-environmental agreement and therefore subject to management restrictions.

Cattle production was the most profitable activity on all mixed livestock crofts, generating an annual revenue of over £8600 per crofter on the Uists and more than £1700 per crofter on Harris during the reference period (Table 5.4). The bias towards store lamb production suggests that this activity was preferred to cattle production, however, it was a much less profitable activity and resulted in negative gross margins for all crofters during the reference period (Table 5.4). This is in huge contrast to the gross margins achieved through cattle production, which were equal to a mean of £2795 crofter⁻¹ and £1113 crofter⁻¹ on the Uists and Harris respectively. However, despite these losses, the inputs required for sheep production were often much cheaper (*e.g.* £2457 crofter⁻¹ *c.f.* £5798

crofter⁻¹ on the Uists) , and the time required to produce sheep is much less (4.2 hours sheep⁻¹ year⁻¹ v.s. 12 hours cow⁻¹ year⁻¹, Beaton *et al.*, 2007). This is particularly relevant as many of the crofters operating mixed livestock crofts were estimated to be over the age of 60 and stated that they found cattle production increasingly difficult due to reduced physical ability.

Crofters on Lewis focused on the production of store and fat lambs. Crofts on this island were smaller than elsewhere in the study area, therefore production and revenue were much reduced compared to mixed livestock crofts (Table 5.3). Interestingly, the average market price received for store lambs was approximately 30% less than that reported by crofters on either the Uists or Harris. Purchasing feed accounted for a large proportion (49%) of the variable costs associated with sheep production and, in line with results from the other islands, production resulted in negative gross margins. However, losses incurred were, on average, less than those experienced by crofters in the rest of the study area (Table 5.4).

Across the sample, labour primarily came from the crofter with additional help from immediate family members. None of the crofters or their family received a wage in return for their time spent working on the croft. Any full-time work was carried out by the crofter themselves, with 78% of Uist crofters and 33% of Harris crofters working on their crofts full time. In contrast, crofters on Lewis worked purely on a part-time basis. Diversification and off-croft work accounted for the remainder of the crofters' time. Some activities were contracted out on the Uists and Harris on a part-time basis. Contractors were employed to help with silage production by all crofters on the Uists, although stock management and ploughing are other activities where contractors were often hired. The

mean rate for silage production was approximately £70 day⁻¹ or between £3-9.50 bale⁻¹. Day rates for stock management were the same as for silage.

The number and range of machinery kept varied between islands, although certain types of equipment were owned by the majority of crofters throughout the study area. For example, 89% of crofters owned at least one tractor. Machinery owned by Harris crofters was limited to a tractor, plough, harrow and associated small implements. This contrasts noticeably with the Uists where livestock trailers, ploughs, fertilizer spreaders and mowers, in addition to an average of two tractors, were owned by over 44% of crofters. Other equipment associated with silage production, such as balers and bale wrappers, were also owned by several Uist crofters and a similar range of equipment was kept by crofters on Lewis. The value of croft machinery varied between the islands with the average price per unit much greater on the Uists than Lewis. However, tractors and silage equipment were consistently the most valuable items owned.

A variety of subsidy payments and agri-environmental payments were available to crofters across the study area and contributed to a large proportion of croft revenue (Table 5.4). Crofters on Lewis received the greatest financial assistance, with 86% of agricultural revenue derived from subsidies. Although this value was much less on the Uists and Harris, payments still accounted for 59% and 69% of crofting revenue on each island. The Single Farm Payment (SFP) and Less Favoured Area Support Scheme (LFASS) were received by all crofters throughout the study area. The SFP was the largest subsidy received and accounted for between 20%-27% of total revenue, on average, across all islands and croft types. The LFASS also made a significant contribution to revenue throughout the study area, contributing to between 12-20% of croft revenue. In contrast, where subsidy schemes were voluntary, participation varied between the islands. For

example, 67% of crofters on the Uists and Harris participated in the Rural Stewardship Scheme (RSS) compared to 14% on Lewis. Similarly, 89% of Uist crofters undertook activities under the Land Management Contract Menu Scheme (LMCMS) whereas only 29% participated on Lewis and none on Harris. However, for those crofters who did take part in the scheme on Lewis, it contributed to nearly 50% of their annual croft revenue. A number of crofters on each island also received a small contribution to their incomes from the Scottish Beef Calf Scheme (SBCS) and the Crofting Counties Agricultural Grant Scheme (CCAGS) (Table 5.5).

For a large proportion of crofters in this study crofting was not their main source of income. On Lewis crofting only contributed to $\leq 10\%$ of the crofter's total household income in 86% of cases. Similarly, Harris crofters estimated that only $\leq 20\%$ of their household income was derived from crofting activities. In general the remaining income was generated through off-croft activities (*e.g.* employment with the local council) or, through diversification activities, such as managing a B&B or letting holiday cottages. In contrast, crofting made up over 80% of household income for 44% of crofters on the Uists and over 40% for an additional 11% of crofters. The remaining household income on the Uists came from off-croft activities, including part-time work as an undertaker and with the local water board. Only 11% of crofters received any income from diversification. The overall mean revenue, variable costs and gross margins varied hugely between the different islands as illustrated by the large positive gross margins achieved by crofters on the Uists and Harris compared to crofters on Lewis (Table 5.4). As crofting on the Uists was on a greater scale than the other study areas it is unsurprising that crofters on these islands achieved the greatest gross margins for their crofting activities.

Table 5.3. Mean livestock numbers for each island. ± 1 S.E. is shown in brackets.

Island	Mean croft area (ha) (excluding common moorland grazings)	Cattle	Sheep
The Uists	55 (± 18)	192 (± 29)	192 (± 29)
Harris	18 (± 12)	9 (± 3)	178 (± 54)
Lewis	8 (± 3)	0	40 (± 5)

Table 5.4. The input costs and output prices for crofting activities in the Outer Hebrides shown as £ crofter⁻¹. ± 1 S.E.

	Uists		Harris		Lewis	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Variable Costs						
<i>Sheep production</i>						
Fodder	1272	587	705	555	217	43
Medicines, Dips & Veterinary Treatment	517	146	477	423	103	36
Haulage, Tags, Levies, Shearing, Scanning & Commission	668	203	543	474	124	40
<i>Cattle production</i>						
Fodder	2535	832	587	279	-	-
Veterinary Treatment & Medicines	575	166	120	43	-	-
Commission, Haulage, Tags & Levies	1150	333	240	86	-	-
Fertilizers	902	294	-	-	-	-
Silage production	1266		-	-	-	-
Bull hire	370	0	0	0	-	-
Revenue						
Sheep production	2289	884	1230	1170	317	121
<i>Cattle production</i>						
Sales	8684	3063	1703	677	-	-
Scottish Beef Calf Scheme (SBCS) Payments	909	192	354	143	-	-
Subsidies						
Single Farm Payment (SFP)	7726	2801	2645	2180	557	257
Rural Stewardship Scheme (RSS)	4263	659	2650	50	0	0
Land Management Contract Menu Scheme (LMCMS)	1036	246	0	0	1100	100
Less Favoured Area Support Scheme (LFASS)	4115	1723	2174	1663	257	91
Gross Margins						
Sheep production		-168		-495		-127
Cattle production		2795		1113		-
Total croft		19767		8040		1787

Table 5.5. The payment schemes available to crofters throughout the study area and a description of the nature of the scheme (Beaton *et al.*, 2007). Crofters in this study only participated in schemes 1-6, although the remaining schemes were also available to them.

Scheme	Description
Single Farm Payment Scheme (SFPS)	Direct government support scheme introduced in January 2005 following reform of the EU's Common Agricultural Policy (CAP). Area based payment based on historic claims made between 2000-2002. Farmers or crofters paid under any production based support schemes during this period were allocated entitlements which could be activated after 2005. In order to receive the SFP, all entitlements held must be accompanied by an eligible hectare of land and are subject to the claimant meeting cross-compliance regulations
Less Favoured Area Support Scheme (LFASS)	Area based support scheme implemented in Scotland as part of the Scottish Rural Development Plan from 2007-2013. Benefits farmers and crofters in designated Less Favoured Areas (LFAs). Claimants must declare a minimum of 3 ha of eligible land, which is actively farmed for at least 183 days in the period claimed for. Subject to cross-compliance
Rural Stewardship Scheme (RSS)	Agri-environment scheme in operation prior to the Land Management Contracts (LMC) system. The scheme closed to applications in April 2006.
Land Management Contract Menu Scheme (LMCMS)	Tier 2 of the Land Management Contracts (LMC) system introduced in Scotland in 2005 and closed to new applicants in 2007. The aim of this scheme is to deliver economic, social and environmental benefits. Now referred to as Rural Development Contracts – Land Managers Options (RDC LMO) in the new Scottish Rural Development Programme 2007-2013
Scottish Beef Calf Scheme (SBCS)	Direct support payments to farmers and crofters producing beef in Scotland. Scheme introduced in January 2005. Payment made for male and female calves which are at least 75% beef bred. Calves must have been born on a Scottish holding and kept there for at least 30 days. The first 10 eligible animals receive a higher payment rate than all subsequent calves. During the reference period in this study (2007) the higher payment rate was £73.46 head ⁻¹ and £36.73 head ⁻¹ for the lower payment
Crofting Counties Agricultural Grants Scheme (CCAGS)	Administered by the Crofters Commission, the scheme aims to support to crofters to ensure the viability and sustainability of crofting. The scheme supports land improvement, construction of agricultural buildings, access and services for rearing livestock.
Highlands and Islands Croft Entrant Scheme (HICES)	Delivered by the Crofters Commission and Highlands and Island Enterprise (HIE), this scheme provides practical and financial support to young people to encourage them to remain in crofting, and promotes the release of crofts from inactive crofters to new croft entrants
Crofting Community Development Scheme (CCDS)	Encourages crofting communities to improve the marketing of their produce without increasing output, improve communication between communities, and other aspects of community improvement, including the adoption of environmentally beneficial land management
Crofters Cattle Quality Improvement Scheme (CCQIS)	Provides a 50% grant towards the hire or purchase of bulls for crofting groups to enhance the genetic quality of their beef herds. Maximum grant of £2000, and bulls supplied through the Department Stud Farm, administered by the Crofters Commission
Croft House Grant Scheme	Grants to improve and maintain the standards of croft housing. Scheme is aimed at younger, more active crofters to encourage them to remain in the region

5.5. Discussion

5.5.1. General changes to crofting

Historically, crofters were responsible for the management of their own crofts (Stewart, 2005). However, this is now rarely the case and it is common for crofters to manage several crofts simultaneously (Willis, 2001; Stewart, 2005). For example, there are currently around 17,000 registered crofts but only 10-12,000 associated households (Stewart, 2005). Multiple tenancies were a frequent occurrence in this study, particularly in the Uists where crofters managed an average of two additional crofts over and above their own home croft. Traditionally, crofts were small agricultural units, often covering an area of less than 2.5 ha (Willis, 1991). However, due to this increase in multiple tenancies throughout the Crofting Counties the average croft size has increased accordingly (Caird, 1979). This is apparent on the Uists where crofts covered a mean area of 55 ha, and increased to an average of 109 ha when shares of rough grazings were included. This finding is similar to Sutherland and Bevan (2001), who found that the total area managed per crofter rose from 104 ha in 1988/89 to 116 ha in 2000. My results suggests that this trend is currently continuing in the Outer Hebrides. Following discussions with crofters on the Uists it appears that an aging population and the subsequent reduction in the number of physically able crofters are important drivers of this change. This is corroborated by recent statistics which show that 29% of the total Hebridean population fell within the 49-64 age bracket in 2007 and that 33% of the population are predicted to be over the age of 65 by 2031 (Comhairle nan Eilean Siar, 2009a,b), and is also noted by Willis (1991; 2001).

The influence of an aging population extends beyond socio-economic issues to impact on the natural environment of the Outer Hebrides. For example, due to age and reduced physical ability 47% of the crofters surveyed were intending on scaling down production, or at least maintaining it at current levels, in the near future. Similarly, Sutherland and

Bevan (2001) found that crofters in their survey were intending on simplifying or extensifying their activities. Interestingly, however, Sutherland and Bevan (2001) also identified a trend towards intensification, so whilst some crofters were scaling down operations this was more than compensated for by a smaller number of crofters significantly increasing their livestock numbers. The general consensus from crofters in my survey was for a reduction in sheep numbers on their crofts over the next two years. However, it has already been noted in the literature that throughout crofting areas inbye land is being turned over to sheep grazing (Willis, 1991), and this was particularly evident from the results on Lewis. Worryingly, this island had a low density of foraging bumblebees in the ecological study (Chapter 2), and was the only island in the study where crofters expressed an intention to increase their sheep numbers. The results of the ecological study also highlight the negative impacts of sheep grazing on bumblebee abundance. Consequently, simplifying crofting to a sheep based system in such a marginal agricultural area will have serious impacts on bumblebee populations and other biodiversity associated with the semi-natural grasslands in this region. In addition, changing land management practices could potentially affect other factors such as tourism (Sutherland and Bevan, 2001) which may, in turn, have a negative effect on the region's economy to which tourism contributed over 15% of Gross Regional Domestic Product (GRDP) in 2006 (Comhairle nan Eilean Siar, 2009a).

5.5.2. Changes in croft management

It is not possible to determine how croft management has changed over time from this study alone. However, when compared to the literature available it is possible to identify some of the changes that have occurred in the study area during the twentieth century. The most notable changes have been to the number and breeds of livestock reared (both sheep and cattle) and the extent to which arable practices contribute to current crofting activities.

Traditionally, cattle production varied throughout the Outer Hebrides with only crofters on Barra and the Uists grazing the machair and rearing cattle on a commercial basis (Hance, 1952). Elsewhere, crofters commonly had one or two house cows which provided the family with a personal supply of dairy produce (Hance, 1952). The results of this study suggest that this form of subsistence has declined, although not disappeared, on Lewis and Harris, and demonstrate that the commercial rearing of beef herds is still an important aspect of crofting on the Uists. However, the traditional Highland breed that was produced during the first half of the twentieth century has now been replaced by continental breeds such as Limousin and Simmental, which are more commercial breeds and allow crofters to compete in the UK market.

The proportion of crofts producing cattle throughout the Crofting Counties was found to have declined from 74% to 31% between 1990 and 2000, and over 50% of crofters had reduced or sold their beef herds (Sutherland and Bevan, 2001). Although none of the crofters surveyed on the Uists intended on abandoning cattle production altogether, the decreasing number of active crofters on these islands points towards a continuation of this trend. Sutherland and Bevan (2001) also recorded an intensification of production on crofts where cattle remained. This contrasts with my results for the Uists which show that 37% of crofters had decreased the number of cattle on their crofts since 2000 and over 87% were intending on decreasing their cattle numbers further, or would at least maintain their current herd sizes during the next couple of years. Again this, coupled with an aging crofting population, suggests that cattle production on the Uists is undergoing a reduction in its intensity, which generally corresponds with other crofting areas (Willis, 2001).

Sheep production today is markedly different from early sheep rearing practices. The mean number of sheep reared in this study was 119 crofter⁻¹ and this varied greatly

between the islands. Despite these differences, sheep numbers were consistently higher in this survey than the 20-30 sheep crofter⁻¹ recorded by Hance (1952). Sutherland and Bevan (2001) also found a 25% increase in numbers between 1988/89 and 1998. These differences are likely to be accounted for by the increase in effective croft size that has arisen from multiple tenancies (Caird, 1979), and by changes in sheep production methods from wool for use in the tweed industry to the production and export of store lambs to the mainland (Hance, 1952; Willis, 1991). With the increase in sheep numbers has been a change in grazing regimes: originally sheep were put to the rough grazings and crofters with shares in sheep stock clubs would employ a shepherd to tend the animals as one flock (Hance, 1952; Willis, 1991). However, socio-economic factors have led to a trend towards sheep grazing on the inbye rather than the hill (Willis, 1991). Traditionally, shepherds would have been employed to supervise the grazings during the summer and round up the sheep. However, this role has disappeared from many areas as it is now too expensive to maintain. Consequently, the onus is now on the crofters to move and gather their own flocks. However, elderly crofters often find it too difficult to move their livestock and resort to keeping sheep on the inbye throughout the year (J. Mather, pers. comm.; Willis, 1991). In addition, the migration of young people away from the region has resulted in few young able people taking up crofting, thus perpetuating this problem. This was commonly found in my study, with only 21% of crofters moving sheep from the inbye to rough grazings during the summer. The subsequent consequences of overgrazing the inbye on biodiversity were clear from the ecological study carried out in Chapter 2. As with cattle, sheep breeds reared have changed over time with the Hebridean Blackface now largely replaced by Suffolks, Texels and other similar commercial breeds. These breeds were frequently found on Lewis where they had often been crossed with the traditional Blackface. However, North Country Cheviots and Blackface were the most common breeds throughout the remainder of the study area.

Arable activities undertaken on crofts have also evolved over time in response to increased mechanisation. The replacement of horses by the tractor led to a reduction in the amount of land that could be cultivated in the Uists as tractors were unable to navigate the difficult terrain (Caird, 1979). This area has continued to decline with the average area of crops cultivated throughout the various crofting regions of Scotland estimated at only 0.5 ha croft⁻¹ (Sutherland and Bevan, 2001). Cultivation of fodder crops remained an important activity for the crofters on the Uists. Although the most commonly grown crops were mixed cereals, grasses were also frequently cultivated. This reflects the transition in fodder production on the Uists from meadow hay to sown hay (Hance, 1952; Caird, 1979), and then to silage and winter feed production (Willis, 1991). This move towards more intensive arable production has been observed throughout the crofting region with the area of permanent grass and improved grassland increasing during the 1990s (Sutherland and Bevan, 2001), and apportionment of common grazings has resulted in the improved productivity of this land type (Crofters Commission, 1991). Due to the decline in cattle numbers on crofts, the availability of farmyard manure has declined and the use of artificial fertilizers has subsequently increased (Hance, 1952). Fencing of pastures and reseeded to increase grass quality have also increased (Caird, 1979; Willis, 1991). All these factors were also evident in this study.

5.5.3. *Croft economics*

Crofting was originally designed in such a way as to ensure that crofters could not be self sufficient and would need to rely on a supplementary income in order to meet their rents (Willis, 1991; Stewart, 2005). This is still the case today: in 1990 only 5% of crofters were recorded as being employed full time on the croft (Willis, 1991), and in my survey all crofters on Lewis had additional sources of income other than that generated by agriculture. Therefore, it was not surprising that the estimated total croft income was

≤10% of the total household income for crofters on this island. Sutherland and Bevan (2001) also found that crofting activities contributed to a very small proportion of household income although their figures were much lower (<1% in 1998 c.f. 9% in 1988/89). Crofting on the Uists showed the opposite pattern with 44% of crofters receiving over 80% of their household income from agricultural activities. This is in contrast to the regional trend recorded by Sutherland and Bevan (2001) and also the results I obtained for Lewis and Harris. It seems likely that the greater dependence on income from crofting on the Uists originates from the more commercial nature of crofting activities that historically took place and still persist on these islands. This may also explain the lesser degree of diversification observed when compared to Harris and Lewis, where diversification is more common and make a notable contribution to total household income.

The mean gross margins derived from crofting activities per crofter in this study ranged from £19,767 on the Uists to only £1787 on Lewis. Even taking into account rough estimates of the fixed costs, net income on the Uists is estimated to be much greater than the £1000 crofter⁻¹ recorded in 1999 by Sutherland and Bevan (2001). Crofters on the Uists do operate on a greater scale than crofters on the other islands of the Outer Hebrides, therefore it is possible that the more commercial nature of crofting on these particular islands are anomalous when compared to crofting throughout the remainder of the Crofting Counties.

The variable costs associated with livestock and crop production often equated to a large proportion of the revenue generated by agricultural activities, and accounted for 73% of the mean revenue generated by livestock sales in the study area. Sutherland and Bevan (2001) recorded variable costs of £3139 crofter⁻¹ in 1999 and these were much higher than those

calculated by Kinloch and Dalton (1990) in 1989. Between 1989 and 1999 Sutherland and Bevan (2001) attributed higher variable costs to an increased dependency on imported fodder along with an 85% increase in fodder prices. The mean amount spent on purchasing fodder during the reference period in my survey varied between £3807 – £217 crofter⁻¹ and accounted for between 46% – 48% of all variable costs incurred throughout the region. This implies that the continued reliance on bought-in fodder inevitably has a significant impact on the profit margins crofters achieve in the Outer Hebrides. In addition, it is likely that profit margins for crofters are reduced by the type of livestock production they undertake. Because crofters are limited to store lamb and beef production the market price they receive for their produce is relatively low compared to that which is received by the lowland farmers who fatten and finish the animals purchased (Willis, 1991). In addition, the market price of store lambs has fluctuated greatly in recent years which increases the economic uncertainty associated with sheep production. This is clearly demonstrated by crofters persevering with sheep production despite the negative returns from this activity during the reference period. However, an increase of 17% in the market price of store lambs received by Uist crofters would generate positive gross margins, therefore sheep production could become a worthwhile activity when considered over a longer period.

The majority of crofters in the Uists and Harris received an additional boost to their incomes through participation in AES. Greater participation on the Uists resulted from a greater awareness of the benefits of AES, as many of the crofters had been involved with the Uists Environmentally Sensitive Area (ESA) scheme prior to their current AES agreements. This was also found by Sutherland and Bevan (2001). However, when investigating the most influential factors on croft management decisions they discovered that 53% of crofters thought direct payments were unimportant, whilst 79% thought AES

payments were unimportant. This may explain the lack of uptake of schemes on Lewis. It also appears that this negative attitude towards payments still exists in the Outer Hebrides: only 44% of crofters who were aware of the latest AES expressed an interest in participating. Interestingly, 80% of those were crofters on the Uists. The most commonly cited reason for not participating was the administrative burden of the application process and the negligible perceived benefits of the scheme. These transaction costs are particularly limiting for crofters as they operate relatively small agricultural businesses and do not have the ability to absorb such costs (Falconer, 2000).

5.5.4. Conclusion

Crofting has always been an unviable agricultural enterprise due to the small size of the croft units and the unproductive nature of the land (Hance, 1952; Caird, 1979; Willis, 1991; Stewart, 2005). This continues today despite a high degree of financial assistance. The importance of direct payments and AES are therefore increasingly important. However, the crofters' apparent lack of enthusiasm and negative attitude towards the new Rural Priorities AES within the latest Scottish Rural Development Programme (SRDP), even on the Uists where such schemes have been met favourably in the past, has significant implications for the future of croft management and consequently the biodiversity associated with crofting practices in this region. Schemes which are specific to the Outer Hebrides need to be developed urgently in order to preserve the unique nature of the crofting system and its associated biodiversity. Potential schemes need to benefit, and therefore appeal, to the crofting community as well as conservationists, and provide a significant benefit for involvement whilst minimising both the actual and perceived transaction costs. A simplified application process and competition for agreements limited to the Crofting Counties rather than with other farming systems on the Scottish mainland would improve the crofter's chances of acceptance into a scheme and boost confidence in

AES on the whole. A new scheme specific to crofting urgently needs to be developed in order to be included in the forthcoming rural development plan in 2013.

Appendix I – Crofter Survey

Section 1 – Croft History

- 1.1. Are you the tenant or owner of the croft? (Please circle) Tenant Owner
- 1.2. How long have you had the croft?.....years
- 1.3. Is the croft actively managed? Yes No
- a. If yes, how long has the croft been managed?.....years
- b. If no, how long since there has been any active management?years
- 1.4. Is the management of the croft leased to contractors? Yes No
- 1.5. Do you lease your common grazing rights?
- 1.6. Do you manage any other crofts? Yes No
If yes, how many?.....

Section 2 – Croft Management

- 2.1. What is the total area of the croft/s?ha
- a. What area/proportion of this is:
- Machair..... ha, or%
- Semi-improved grassland..... ha, or%
- Improved grassland..... ha, or%
- Rush pasture..... ha, or%
- Rough grazing..... ha, or%
- b. Is any of the croft within designated areas (e.g. SSSI, SAC, etc.)?
- SSSI.....ha, or%
- SAC.....ha, or%
- SPA.....ha, or%
- NNR.....ha, or%
- RSPB nature reserve.....ha, or%
- 2.2. Do you grow crops on the machair? Yes No
- a. Are crops grown for commercial use? Yes No Both
- b. What did you grow in 2007?

Crop type		Area (ha)	Yield (t/ha)	Fertilizer – NPK (kg/ha)	Manure (t/ha)	Seaweed (t/ha)
Commercial						
Home grown fodder						
Home grown vegetables						

c. What sequence of rotation do you use? Please specify:

.....

2.3. Did you buy in any feed in the last 12 months? Yes No
If yes, how much did you buy?

Type of Feed	Amount (t)		Price (£/t)	
	Sheep	Cattle	Sheep	Cattle
Concentrates				
Straights				
Hay				
Silage				
Straw				

2.4. Do you use fertilizers, manure or seaweed? Yes No
If yes, please specify how much and when. Please also specify cutting dates.

Land Type	Amount and application date									Cutting Dates
	Fertilizer - NPK			Manure			Seaweed			
	Ha	Kg/ha	Date	Ha	Kg/ha	Date	Ha	Kg/ha	Date	
Machair										
Semi-improved grassland										
Improved grassland										
Rush pasture										
Rough grazing										

2.5. Do you keep sheep? Yes No
a. If yes, what breeds do you keep?.....
b. If yes, what number did you have in 2007?

Breed of Sheep	Breed:		Breed:	
	Number	Average price £/head	Number	Average price £/head
Store lambs for sale				
Fat lambs for sale				
Draft ewes for sale				
Live lambs born on croft				
Lambs still on croft				
Breeding ewes put on the ram last autumn				
Home bred replacement ewes				

c. How have sheep numbers changed on the croft since 2000? Increased Decreased
Stayed same

- d. What percentage of sheep are: exported to the rest of the UK.....%
 exported internationally.....%
 sold locally.....%
 kept on the croft.....%

2.6. Do you keep cattle? Yes No

- a. What system of beef production do you use? Please indicate the approximate numbers in each category.

	Numbers	Breed
Suckler cows		
Calves sold on as store cattle		
Calves finished on farm		

- b. How have cattle numbers changed on the croft since 2000? Increased Decreased
 Stayed same

- c. Please could you indicate the number and price of cows/calves sold at market for the following ages in the past 12 months?

	Number	Price (£/head)	Direct sale (%)	Auction sale (%)
<3 months				
11 months				
18 months				
2 years				
> 2 years				

- d. What percentage of cattle are: exported to the rest of the UK.....%
 exported internationally.....%
 sold locally.....%
 kept on the croft.....%

- 2.7. Please specify which grazing regime you follow and indicate the dates stock are put onto and removed from the machair.

Regime	Sheep		Cattle	
	Yes	No	Yes	No
Winter grazing on machair				
Spring/summer grazing on machair				
Moorland (common) grazing summer				
Date removed from machair				
Date put on machair				

- 2.8. How many people work on your croft?

	Full Time	Part Time	Hours/Year	Wage
Family Unpaid				
Family Paid				
Hired Labour				

2.9. What activities do you contract out on your croft?

Operation	Unit (hours, days, etc.)	Costs (£/unit)

2.10. Do you own or hire any machinery for the croft? Yes No
If yes, please specify below.

Machine	Own/Hire	Number	Valuation (per unit)

2.11. What percentage of your household income comes from the following sources?

Income Source	% of total croft income
On croft	
Diversification	
Off farm	

2.12. Please give details of diversification and off-croft activities. (e.g. B&B, etc.)

.....

2.13. In the next two years are you planning to change any of the following?

Sheep	Increase	Decrease	Stay the same	N/A
Cattle	Increase	Decrease	Stay the same	N/A
Arable	Increase	Decrease	Stay the same	N/A
Diversification	Increase	Decrease	Stay the same	N/A

Section 3 – Subsidies

3.1. Do you take part in any of the following agri-environment/grant schemes?
If yes, how much payment did you get this year?

Scheme	Participate (Y/N)	Payment in 2007 (£)
Rural Stewardship Scheme		
Environmentally Sensitive Areas		
RSPB Management Agreement		
Less Favoured Area Support Scheme		
Land Management Contract Menu Scheme		
Hill Livestock Compensatory Allowance		
Scottish Beef Calf Scheme		
Goose Management Scheme		
Single Farm Payment		
Crofting Counties Agricultural Grant Scheme		

3.2. Rural Stewardship Scheme (RSS)

a. What activities do you do to comply with RSS options? Please list the 5 most costly.

Activity	Labour required (hours/year)	If contractor (cost-£)

When does your RSS agreement end?

b. Are you planning on entering the new Rural Development Contract Scheme in the future?
Yes No

3.3. Environmentally Sensitive Areas (ESA)

Please indicate which ESA Tier you are in and with how many hectares/meters.

Tier 1.....ha/m

Tier 2.....ha/m

Please use this list as a prompt for the main ESA options:

- **Cropping** (without or without seaweed)
- **Wetland management**
- **Species rich management**
- **Fallow payment** (two years cropping on machair followed by fallow)

What activities do you do to comply with ESA tiers? Please list the 5 most costly

Activity	Labour required (hours/year)	If contractor (cost-£)

When does your ESA agreement end?

3.3. Land Management Contract Menu Scheme (LMCMS)

Please use this list as a prompt for the main LMCMS options:

- **Animal Health and Welfare Management Plan**
- **Membership of quality assurance and organic certification schemes** (*e.g.* membership of Specially Selected Scotch Farm Assurance Scheme – Cattle and Sheep, Farm Assured British Beef and Lamb Scheme, Scottish Organic Producers Certification Scheme, etc.)
- **Training** (*e.g.* training courses for business skills, opportunities for expanding into other activities).
- **Buffer Areas** (*e.g.* borders in arable fields)
- **Management of Linear Features** (hedgerows, ditches and dykes)
- **Management of Moorland Grazing**
- **Management of Rush Pasture** (*e.g.* aftermath grazing, cutting)
- **Biodiversity cropping on in-bye** (*e.g.* spring sown cereals, fodder roots or fodder rape)
- **Retention of Winter Stubbles** (*e.g.* no cultivation before 28th February)
- **Wild Bird Seed Mix**
- **Summer Cattle Grazing** (*e.g.* stock turned out onto rough grazings before June 1st and kept out for 3 months)
- **Nutrient Management** (*e.g.* soil testing for pH, nutrient status and trace element levels)
- **Improving Access** (*e.g.* path maintenance)

What activities do you do to comply with LMCMS options? Please list the 5 most costly

Activity	Labour required (hours/year)	If contractor (cost-£)

3.4. RSPB Management Agreements

- a. What activities do you do to comply with your RSPB Management Agreement?
Please list the 5 most costly.

Activity	Labour required (hours/year)	If contractor (cost-£)

When does your management agreement end?

- b. Are you planning on entering more RSPB management schemes in the future?
Yes No

3.5. The SRDP and Rural Development Contracts

- a. Are you aware of the new SRDP? Yes No
- b. Are you aware of the new RDC (Rural Priorities) agri-environment scheme? Yes No
- c. If Yes, are you intending on applying to the scheme? Yes No

If no, please explain why

.....
.....
.....
.....
.....
.....
.....

Many thanks for your time and your help.

Chapter 6: The trade-off between agriculture and biodiversity in marginal areas: Can crofting and bumblebee conservation be reconciled?

The work presented in this chapter forms the basis of the paper: Osgathorpe, L.M., Park, K., Goulson, D., Acs, S. & Hanley, N., 2011. The trade-off between agriculture and biodiversity in marginal areas: Can crofting and bumblebee conservation be reconciled? Ecological Economics. 70(6): 1162-1169.

6.1. Abstract

Crofting is a low intensity agricultural system typified by small scale mixed livestock production and rotational cropping activities. As with other low intensity farming systems across Europe, crofting is changing in response to a range of socio-economic factors. This is having a negative impact on the populations of rare bumblebees that are associated with this agricultural system. In this chapter I use an ecological-economic modelling approach to examine the likely impacts of introducing two different management options for conserving bumblebees on croft land use and income. Two linear programming models were constructed to represent the predominant crofting systems found in the Outer Hebrides, and varying constraints on bumblebee abundance were imposed to examine the trade-off between conservation and agricultural incomes. The model outputs illustrate that in some instances it is likely that both agricultural profits and bumblebee densities can be enhanced. Re-establishing the traditional practice of summer moorland grazing is predicted to increase croft profits in addition to enhancing bumblebee populations on mixed livestock crofts, suggesting that advocacy rather than Agri-Environment Schemes (AES) is likely to be the most effective approach for bumblebee conservation. Wildflower seed mixes are often recommended for improving bumblebee populations in agricultural landscapes. This method is predicted to be most effective on sheep based crofts, although this incurs a cost to the crofter and would require a payment scheme to compensate for

income forgone. I conclude that policy-makers should take into consideration the type of farming system when designing cost-effective agri-environment policies for low intensity farming systems.

6.2. Introduction

Changing agricultural practices during the latter half of the twentieth century have been identified as an important determinant of declines in a wide range of farmland biodiversity (Chamberlain *et al.*, 2000; Donald *et al.*, 2001; Robinson and Sutherland, 2002). Population declines have been recorded in species belonging to a variety of taxonomic groups, ranging from birds and butterflies to plants (Robinson and Sutherland, 2002). Agricultural intensification has also affected populations of pollinating insects, including a number of bumblebee (*Bombus*) species which have declined throughout the UK and western Europe (Goulson, 2003a; Goulson *et al.*, 2008a). Bumblebees are frequently associated with wildflower-rich semi-natural habitats, such as permanent unimproved grassland, which provide essential foraging resources (Williams and Osborne, 2009). However, many of these habitats, and therefore the associated forage, have been lost from agricultural landscapes, driving bumblebee declines (Goulson, 2003; Carvell *et al.*, 2006; Goulson *et al.*, 2008a). Consequently, of the 25 bumblebee species native to the UK three are now extinct and a further seven are endangered and included on the UK's Biodiversity Action Plan (BAP). Only six species remain common and ubiquitous throughout the UK (Benton, 2006).

The impacts of agricultural intensification have shaped the distribution of the UK's bumblebee fauna, with distributions of some of the rarest species now restricted to isolated areas in the far north and west of Scotland where agricultural practices have changed less (Goulson *et al.*, 2006). Crofting is the predominant form of agriculture in these areas and

crofted areas provide the last remaining strongholds for two of the UK's most endangered bumblebee species: *Bombus distinguendus* and *B. muscorum* (Goulson *et al.*, 2005; Benton, 2006). Agricultural units in the Outer Hebrides and mainland crofting counties of northern Scotland are known as 'crofts' and commonly consist of small areas of enclosed lowland grassland (inbye) with shared rights to common grazings on machair, a low lying calcareous grassland habitat, and also on moorland (Stewart, 2005). Typically crofts are clustered together forming 'townships' in which crofters implement small scale arable rotations and livestock production. Grazing regimes traditionally consist of the inbye and machair being grazed by livestock during the winter, and the movement of livestock to moorland common grazings in the summer (Moisley, 1962; Hance, 1951; Caird, 1987; Love, 2003). Fertilizer inputs were traditionally limited to seaweed and farm yard manure.

The nature of traditional crofting has resulted in a high value of croft land for conservation, particularly the coastal wildflower-rich machair grasslands (Love, 2003). However, crofting practices are also changing in response to a variety of factors. Artificial fertilizers are used to an increasing degree, hay production has been superseded by silage, sheep numbers have risen dramatically, and the area of permanent and improved grassland has increased (Caird, 1979; Willis, 1991; Sutherland and Bevan, 2001). As with many low intensity farming systems across Europe (Caballero, 2007), a range of socio-economic factors are contributing to the impacts of intensification. For example, the combination of rural depopulation and the increasing age of crofters throughout the region has led to a reduction in the number of crofters actively managing their land, increased the area of rush dominated (and therefore ecologically degraded) land (Crofters Commission, 1991), and perpetuated a trend for sheep production (Willis, 1991). Consequently, many older crofters now view crofting as a purely sheep based system (Willis, 1991). In addition, the number of crofting households fell by 23% throughout the Crofting Counties between the

1950s – 1980s (Crofters Commission, 1991), and now many crofters are responsible for the management of more than one croft, decreasing the mosaic of land-uses characteristic of traditional crofting and reducing the value of croft land to biodiversity. In addition, croft income is now largely dependent on the receipt of a range of agricultural subsidies, including the Single Farm Payment (SFP) (see Appendix II). With the future of such subsidies currently unclear, the sustainability of crofting in the future is uncertain and has serious implications for the biodiversity associated with crofted habitats.

The more intensive management practices now employed on crofts in northwest Scotland are of little value to foraging bumblebees (Chapter 2). Future agricultural policy and socio-economic changes are likely to continue to impact on bumblebee populations. In order for effective conservation measures to be developed, ecological *and* economic factors need to be taken into consideration by policymakers.

In this chapter I use ecological-economic models to examine the likely impacts of introducing bumblebee conservation measures on the allocation of key crofting resources (*e.g.* land, labour, income), and discuss the most cost-effective management options for bumblebee conservation in crofted areas. Trade-offs between croft income and bumblebee densities are identified across a range of bumblebee densities and across croft types. Following a review of the types of ecological-economic models available in Chapter 4, I chose to use Linear Programming (LP) models to simulate croft production decisions. LP models can be used to simulate the impact on land-use at the level of the individual farmer (or crofter in this case) of changes in resources, prices or government policies. Although LP models are subject to several limitations (such as the assumption of rational behaviour on the part of land managers, linearity of constraints, or fixed input-output coefficients), they provide a suitable means of examining the micro-level effects of policy changes on

farmer behaviour across different farm types (Acs *et al.*, 2010). LP models also calculate the marginal value product or shadow price associated with fully utilised resources (Hazell and Norton, 1986). Shadow prices are a useful analytical device since they can represent trade-offs between biodiversity and farm income. In my case they show the marginal cost, in terms of farm profits, of increasingly strict constraints on bumblebee abundance. In other words, shadow prices show the supply price of increasing levels of biodiversity. Ecological data may also be incorporated into these land-use models to examine the impacts on a range of environmental variables (*e.g.* biodiversity, soil erosion, deforestation) of changes in land manager behaviour, and to optimise land management for the benefit of the environment. For example, Carpentier *et al.* (2000) used this method to investigate the impacts of changes in farmer behaviour on farm income and deforestation in the western Brazilian Amazon, whilst Saldarriaga Isaza *et al.* (2007) utilised LP models to examine the relationship between land management practices and huemul (*Hippocamelus bisulcus*) conservation in Chile.

6.3. Methods

6.3.1. Socio-economic croft survey

A croft survey was undertaken to establish which land management practices and production methods are currently employed by crofters in the Outer Hebrides, and to determine which socio-economic factors govern croft management decisions. Socio-economic data from farmers relating to income and land management decisions was required to calibrate mathematical models of farmer behaviour, which would allow me to examine the impacts of conservation measures on farm production decisions. To ensure the relevant data was collected my survey focused on the farming system implemented, the scale of farming operations and the associated input and output prices, and the financial assistance received by farmers. As my data requirements were very similar to those of Acs

et al. (2010), I based my survey on the general structure of the one they used for upland farms in the Peak District, UK. Crofters in the Outer Hebrides were chosen from within the area studied in Chapter 2 to correspond with their survey of bumblebees utilising croft habitats in the region. This enabled me to collect data from a subsample of crofters ($n = 19$) who participated in both the ecological and economic surveys. I interviewed crofters from the islands of North and South Uist, Harris and Lewis during site visits, except for a sub-group (16%) who completed the surveys themselves and returned them by post. All surveys were completed during the spring and summer of 2008. The survey focussed on current management practices, the input costs and output prices associated with agricultural activity, and the subsidies received during the reference period (2007). As crofting practices on both North and South Uist, and Harris were similar, these are collectively referred to as 'the Uists' in the remainder of the chapter, whilst 'Lewis' refers purely to the crofters on that island.

From the survey results I identified two croft types which correspond to the primary production methods utilised by crofters on each island. Store lamb and store calf production with grass and arable silage production was characteristic of the Uists and Harris, although arable production was less common on Harris. Grass crops were primarily cultivated on the improved inbye land, whilst arable cropping consisted of silage cultivated on the machair. Cultivation and fallow periods were organised on a two years cropped, two years fallow rotational basis. In contrast, crofting on Lewis was typified by store lamb production on inbye land. No arable production was carried out and the majority of crofters had no access to moorland grazing, unlike crofters surveyed in the Uists and Harris.

Four land types were identified:

1. *Machair*, a lowland grassland area adjacent to the coast formed from wind-blown shell sand. The sandy soils are low in nutrients and support a diverse variety of wildflowers. The land is primarily used for the cultivation of arable silage and grazing.
2. *Semi-improved grassland*, located on the inbye, forming the main grazings for livestock. Inorganic fertilizers and farm yard manure are applied. This land is also used in the production of grass silage.
3. *Improved grassland*, enhanced with larger amounts of inorganic fertilizers and used for grass silage production.
4. *Moorland*, normally unfenced and often held in common, and to which no inorganic fertilizers or farm yard manure is applied.

All crofters received the Single Farm Payment and payments through the Less Favoured Area Support Scheme (LFASS). Several crofters supplemented this grant income by participating in Agri-Environment Schemes (AES). However, there are currently no prescriptions available in Scotland specifically aimed at conserving bumblebee populations.

6.3.2. *Modelling*

Changes in farmer behaviour in response to changing agricultural policy have been studied using ecological-economic models in a range of settings (*e.g.* Münier *et al.*, 2004; Pacini *et al.*, 2004; Meyer-Aurich, 2005). This approach can be extended to the consideration of conservation issues, with models used to examine the relationship between farm-level decision making and species conservation (*e.g.* Drechsler *et al.*, 2007). I construct two linear programming land-use optimisation models, one for the type of mixed cattle/sheep

and arable crofts found in the Uists and Harris (referred to collectively as ‘Uists’) and one for the sheep crofts found on Lewis.

6.3.2.1. General Approach

Farm production models were used to simulate different conservation scenarios. The general structure of the models is shown in Table 6.1 and takes the form of a standard LP model (Hazell and Norton, 1986), designed to represent the profit maximisation problem of a land manager:

Maximise ($Z = c'x$)

Subject to $Ax \leq b$

And $x \geq 0$

where Z is the gross margin (income from cropping and livestock production net of variable production costs) at the croft level; x is the vector of activities; c is the gross margin or cost per unit of activity; A is a matrix of input use coefficients; and, b is the vector of resource endowments or technical constraints. The activities included in the model are based on typical crofting practices, and are shown by the headings in Table 6.1. Activities are included for different land types, animal production systems, feed production and purchase, fertilizer, hired labour and subsidy payments. The rows of the matrix represent the constraints imposed on croft management in terms of land availability, labour, fertilizer and fodder requirements, and constraints on subsidy payments, *e.g.* activities associated with qualifying for AES payments. The objective function of the LP model is to maximise the total croft business gross margin (profit excluding fixed costs), *i.e.* the total revenue from all activities minus the variable costs associated with all crofting activities. The model output provides the optimal croft production plan, detailing optimal

land allocations, level and type of production, and labour use. All model simulations were carried out in GAMS (General Algebraic Modelling System) version 23.4.

6.3.2.2. *Production Elements*

In the Uists model the beef cattle production element is based on a continental suckler cow calving between February and April with calves sold as store animals (that is, for fattening) between 12-18 months old. This includes 1% cow mortality and 4.5% calf mortality, based on data from the Farm Management Handbook (Beaton *et al.*, 2007). Cattle are generally kept outside throughout the year and their main feed requirements are met through grazing, silage and cattle concentrates. Revenue from cattle production is obtained from direct sales and payments through the Scottish Beef Calf Scheme (SBCS). Variable costs are calculated per head and consist of the purchase of cattle concentrates, the production of silage on the croft and health care. Costs of bull hire are also included, in addition to other costs listed in the Farm Management Handbook (Beaton *et al.*, 2007), such as levies and tags.

In both the Uists and Lewis models the sheep production activities were based on breeding Blackface and North Country Cheviot ewes producing lambs in the spring which are sold as store animals in the autumn. Crofters on Lewis also produced fat lambs and this was included in the Lewis model. Feeding requirements were based on the survey results, with grazing and sheep concentrates comprising the majority of the animals' nutritional needs. Hay was used by some crofters as a supplementary feed. The average number of lambs per ewe was derived from the survey results for each island. No sheep housing requirements were included in the model as this is unusual in the study area. Revenue from sheep production was derived from the direct sale of lambs. Variable costs of production consisted of the purchase of sheep concentrates, hay, healthcare and additional costs (*e.g.*

haulage, levies, tags). Input and output prices for sheep and beef production varied between the models and were based on averages taken from the survey results for each island.

Croft land can be used for different activities within the models. Silage is rarely purchased and home-grown supplies are used to meet the nutritional needs of livestock, above that provided by grazing and concentrates. Improved grassland is used for the cultivation of grass silage crops. Semi-improved land may also be used for this purpose, but is predominantly utilised as grazing for both cattle and sheep. Similarly, machair areas can be used for grazing or growing arable silage (traditionally a combination of barley, oats and rye). Although the crofts commonly have access to shared areas of moorland grazings in the summer, this land was rarely made use of by the crofters in my survey, and is therefore not included in the baseline Uists model or any of the Lewis models. The use of inorganic fertilizers is included as an activity in the Uists model. Usually only one cut of silage is made per year in late July/August. Rotational constraints were also added.

The labour requirements for each activity were based on standard requirements set out in the Farm Management Handbook (Beaton *et al.*, 2007). These requirements could be met by household labour or by hiring contractors. The availability of household labour varied between the islands, with crofters on the Uists often working on the croft full-time and those on Lewis managing their crofts on a part-time basis.

Table 6.1. Matrix showing the general structure of the linear programming farm models for beef and sheep production. The activities included in the model are shown as column headings, whilst the rows represent the constraints imposed on each activity.

<i>Activities</i>	Improved Grassland	Semi-improved Grassland	Machair	Fodder production for own use	Sheep production	Beef production	Hired Labour	Purchase of fertilizer	Purchase of feed	Animal production for sale	SFP	LFASS	AES	Resource endowments and technical constraints
<i>Constraints</i>														
Land requirements	1	1	1											\leq available hectares
Land types for fodder production	-1	-1	-1	1										≤ 0
Fertilizer and manure requirements	+ a_{ij}	+ a_{ij}	+ a_{ij}		- a_{ij}	- a_{ij}		- a_{ij}						≤ 0
Animal production for sale					- a_{ij}	- a_{ij}				+ a_{ij}				≤ 0
Labour requirements				+ a_{ij}	+ a_{ij}	+ a_{ij}	-1							\leq available fixed labour in hours
Feeding requirements				- a_{ij}	+ a_{ij}	+ a_{ij}			- a_{ij}					≤ 0
SFP	+ a_{ij}	+ a_{ij}									- a_{ij}			≤ 0
LFASS	+ a_{ij}	+ a_{ij}										- a_{ij}		≤ 0
AES	+ a_{ij}	+ a_{ij}	+ a_{ij}										- a_{ij}	≤ 0
Livestock constraints for LFASS and AES					+ a_{ij}	+ a_{ij}								\geq minimum livestock unit
Objective function	Costs (£/ha)	Costs (£/ha)	Costs (£/ha)	Costs (£/ha)	Gross margin (£/head)	Gross margin (£/head)	Costs (£/hour)	Costs (£/kg)	Costs (£/t)	Revenue (£/head)	Revenue (£/ha)	Revenue (£/ha)	Revenue (£/ha)	

* a_{ij} – the technical coefficient that relates the activity i to the constraint j

6.3.2.3. Incorporating the ecological data

Relationships between croft land management practices and bumblebee densities have been identified in Chapter 2. All management types found on 22 crofts throughout the Outer Hebrides were surveyed for foraging bumblebees and their forage plants between June-August 2008 (see Chapter 2 for a detailed account of the methods followed). The effect of land management on bumblebee abundance was examined using Generalised Linear Models (GLM) with quasipoisson errors in the statistical software package R, version 2.7.2. Eight management types were surveyed and included in the ecological models: arable, bird and bumblebee conservation seed mix, fallow, silage, summer sheep grazed pasture, summer mixed grazed pasture, unmanaged and winter grazed pasture. Croft land management practices supported low densities of foraging bumblebees; however, management was a significant predictor of bumblebee abundance in all months, with silage, fallow and areas sown with a ‘bird & bumblebee’ conservation seed mix the most beneficial activities. Summer sheep grazing was found to have a particularly detrimental effect on bumblebee abundance. From the GLM results I predicted the median number of foraging bumblebees supported by each management type. We used the data from August when nest development is at its peak and bumblebee abundance greatest. Estimates from the GLMs are incorporated in the LP models as a set of parameters linking bumblebee abundance with the area of each land use (production) activity. This ensures that the density of bumblebees supported by each activity is also simulated and presented in the model output. This provides a numerical link between the profit-maximising pattern of crofting land use and predicted bumblebee abundance.

6.3.2.4. Subsidy schemes available to crofters

Crofters are eligible to receive payments from a wide range of subsidy schemes that include both direct income support payments and agri-environment payments. Direct

subsidy payments were received by all crofters and provide a substantial additional income above that generated by the main production methods alone. In Scotland, the Single Farm Payment (SFP) is based on the average of the historic claims made between 2000-2002. Farmers or crofters paid under any production based support schemes during this period were allocated entitlements which could be activated after 2005. In order to receive the SFP, all entitlements held must be accompanied by an eligible hectare of land and are subject to the claimant meeting cross-compliance regulations. The LFASS is an area based support scheme implemented in Scotland as part of the Scottish Rural Development Plan from 2007-2013, and benefits farmers and crofters in designated Less Favoured Areas (LFAs). Claimants must declare a minimum of 3 ha of eligible land, which is actively farmed for at least 183 days in the period claimed for: this subsidy is also subject to cross-compliance. As all crofters received aid under these schemes, payments were incorporated into the model as a fixed payment per hectare.

Several crofters also participated in Agri-Environmental Schemes (AES) and received payments through these schemes for using environmentally sensitive land management practices. The AES in operation at the time of the survey was the Rural Stewardship Scheme, with management agreements ending in 2010/2011. The primary activities undertaken by crofters in these agreements were management of open and mown grassland, and the implementation of traditional cropping practices on the machair. Payments were also received under Tier 2 of the Land Management Contracts system for implementing Option 1: the Animal Health and Welfare Management Programme. In order to receive payment under an agri-environment agreement, crofters were required to implement some form of management (*e.g.* cropping on machair). Each activity had its own fixed payment rate per hectare and the total payment received was calculated in the model as a function of the area of land under the specified management regime.

6.3.2.5. Model calibration

The models include all aspects of production carried out by crofters in the Outer Hebrides and may therefore be calibrated to represent different scenarios in relation to resources available for crofting in this region. The two croft types (Uists/Harris and Lewis) modelled are based on data derived from the croft survey and are calibrated against the primary production methods (*i.e.* sheep, beef). To ensure that the models are representative of current crofting practices, the livestock numbers were adjusted to the averages from the survey data and key variables were compared between the model outputs and the survey data (Table 6.2). The ‘survey adjusted’ model was implemented to simulate currently observed production patterns. As the purpose of the models is to assess the likely changes in resource use on crofts, the key outputs for this validation process were: gross margin; revenue and variable costs associated with livestock production; and, revenue from subsidies (Table 6.2). Differences emerge between the land-use pattern that would maximise the total farm gross margins and the currently observed pattern of land-use (Table 6.2; discussed below).

Table 6.2. A comparison between the predicted outputs from the optimal (baseline) and survey adjusted models, and the crofter survey data (observed) from the model validation process.

	Optimal (Baseline) Model (£/ha)	Survey Adjusted Model (£/ha)	Observed (£/ha)
<i>Mixed Livestock - Uists</i>			
Revenue Sheep	0	30	32
Revenue Beef	190	169	174
Subsidies	289	285	291
Variable Costs	106	130	135
Gross Margins	373	354	363
<i>Sheep - Lewis</i>			
Revenue Sheep	156	62	61
Subsidies	122	122	120
Variable Costs	141	56	53
Gross Margins	136	128	127

6.3.2.6. *Model scenarios*

To examine the nature of likely trade-offs between the density of bumblebees per croft and croft income, I introduced a series of binding constraints into the LP model on the total number of bumblebees per hectare above that predicted by the baseline model run. Bumblebee density was increased in a step-wise process at increments of 1 bee ha⁻¹ above the baseline for each model. I then examined how crofters should optimally alter their management practices to achieve greater bumblebee abundances and what the consequences for croft income would be. I examined two scenarios based on beneficial management practices identified in the literature (*e.g.* Pywell et al., 2005). The first scenario considered the option of sowing a native wildflower seed mix to attract bumblebees (labelled scenario WM). The seed mix was included in the model as an additional (costly) activity which crofters could choose to include as part of their management regime. The costs involved in this management scenario are subdivided into a one-off capital cost of the initial habitat creation and an annual maintenance cost which would be incurred over the lifetime of the mix (approximately 3-4 years). Devoting land to growing wildflowers also imposes an opportunity cost on the farmer in terms of lost income from alternative uses of this land.

The second scenario considers the impacts of reintroducing moorland grazing in the summer for mixed livestock crofts on the Uists (labelled scenario MG). This scenario was not applicable to sheep crofts on Lewis as crofters in our survey had no access to moorland. The model enabled crofters to choose to use the moorland for grazing during the summer and predicted the optimal land allocations for each activity to achieve the required bumblebee abundances.

6.4. Results

The model calibration process highlights that neither mixed livestock crofters (Uists and Harris) or sheep crofters (Lewis) currently manage their crofts in the most economically efficient way (Table 6.2). In particular, sheep production is less profitable for crofters in mixed livestock systems (in the Uists and Harris) and this activity is removed from the optimal production plan for this croft type. By continuing to produce store lambs, crofters are reducing the croft's gross margins by £18 ha⁻¹, which equates to an annual loss of over £1000 compared to the optimal model. In addition, from a conservation perspective, the model shows that 10% fewer bumblebees are supported by current crofting practices in this system than if crofters were to operate on a profit maximising basis. In contrast, production on sheep crofts in Lewis is lower than the capacity of the available land and sheep stocking densities would be more than double current levels if crofters were profit maximising (Table 6.2). The survey adjusted model for sheep based crofts shows that current management practices provide enough habitat to support low densities of foraging bumblebees (a total of 4.8 bees croft⁻¹ for an average sheep croft of 8 ha). However, increasing sheep production to its maximum capacity would require all land to be brought into production, which would result in the loss of any suitable bumblebee foraging habitat, and therefore a complete loss of bumblebees, from this croft type. The absence of profit maximising behaviour from crofters operating in both crofting systems suggests that additional factors to those included in the models, such as age, play an important part in governing croft management decisions.

6.4.1. Conservation management option A: Planting a wildflower mix on croft land

The predicted impacts of increasing bumblebee abundance on croft gross margins vary between croft types and the method of conservation management used. Incorporating a wildflower seed mix reduces the gross margins achieved by crofters in both croft types,

although the loss of income is predicted to be greatest for crofters on mixed livestock crofts characteristic of the Uists (Fig. 6.1a). There is a trade-off between bumblebee density and croft income, although this threshold varies by croft (Figs. 6.1a-b). Sowing a wildflower mix requires an increase in labour input from the crofter compared to the optimal management plan and, although silage would be a usable by-product of this activity, the opportunity costs incurred through habitat creation alone are substantial – *e.g.* for a 36% increase in bumblebee abundance across the croft (above the optimal model which results in 8.8 bees ha⁻¹), the crofter would need to sow 1.9 ha of wildflower mix and incur an opportunity cost for habitat creation of £666 in the first year. In addition, there would be associated annual maintenance work for the lifetime of the wildflower mix, which again requires added labour inputs. However, as the purchase of seed is not included in the maintenance cost, the opportunity cost associated with 1.9 ha of wildflowers is much less at £54. The opportunity cost comprises the direct costs associated with implementing this practice (buying seed, cost of labour for sowing, ploughing, *etc*), and also the costs of converting the land from one use to another in terms of revenue forgone, *i.e.* from cattle production to wildflowers. Unsurprisingly, purchasing the seed is the most costly element of this practice, with the cost of buying seed accounting for 92% of the direct costs. Stocking rates are also predicted to change under this scenario, with a decline in cattle production (Table 6.3). The absence of sheep from the optimal production plan remains the same. Similarly, introducing a wildflower mix to sheep crofts is also predicted to have a negative effect on the croft gross margins, with sheep numbers predicted to decline as the constraint on bumblebees was tightened (Table 6.3). Interestingly, our model shows that if crofters in sheep based systems on Lewis were currently operating in an optimal manner, they would reduce their stocking densities and the area of grazed land, thereby increasing the area of winter grazed pasture, rather than incorporate a wildflower mix into their management regimes.

6.4.2. Conservation management option B: Use of moorland summer grazing

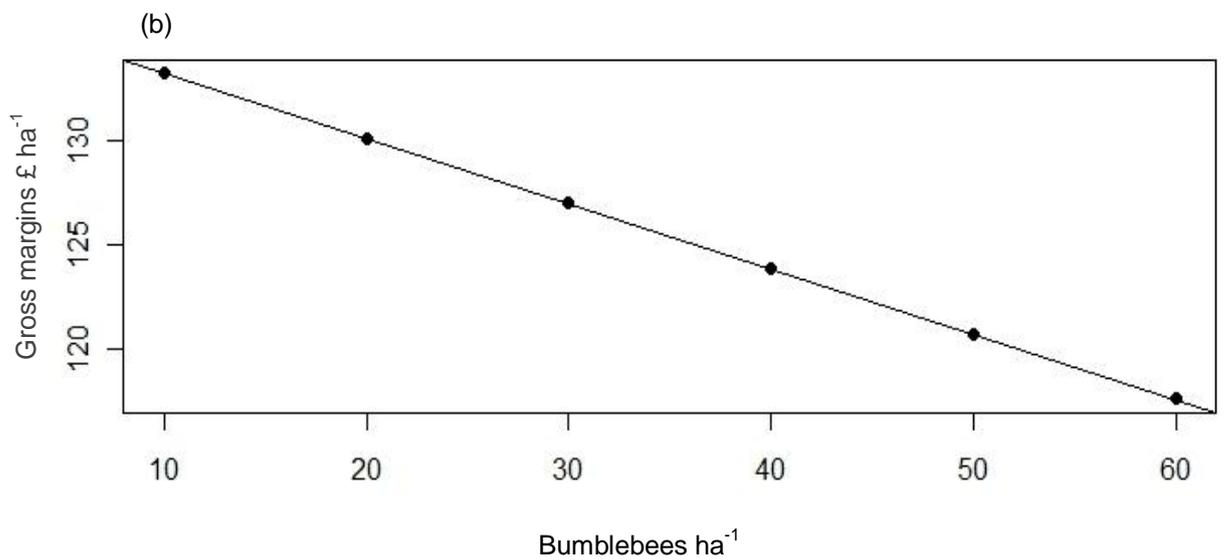
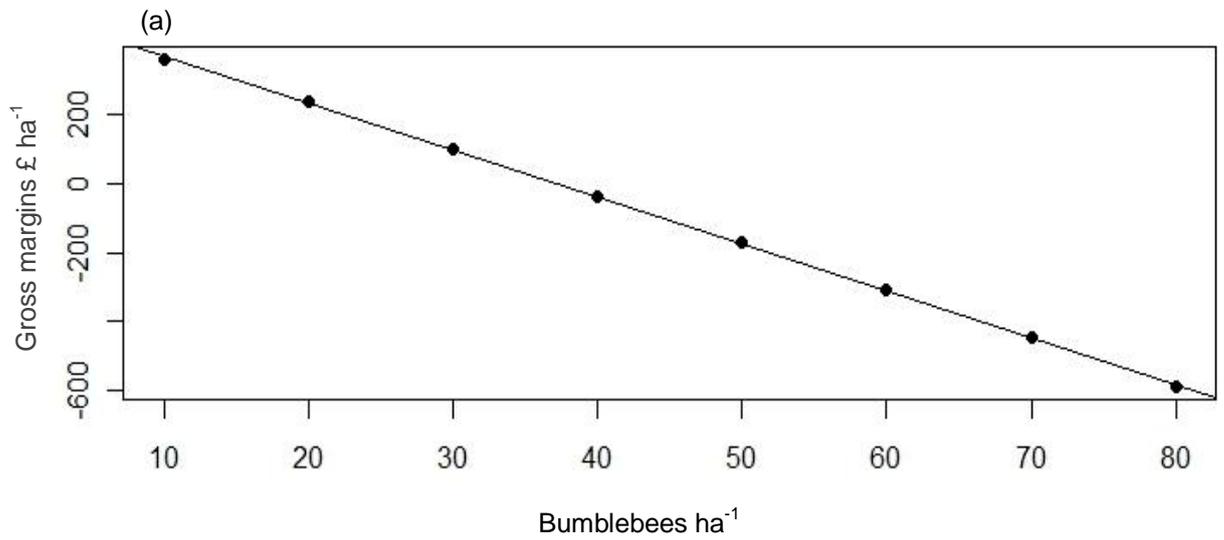
Bringing nearby moorland back into use for summer grazing is predicted to be the most cost-effective conservation method for mixed livestock crofts on the Uists (Table 6.3). Under this scenario, bumblebee abundance increases by 36% above that predicted in the optimal model to 12 bees ha⁻¹ of croft land, and the gross margins received by the crofter increases by 11% to £391 ha⁻¹. However, this management option is somewhat limited as bumblebee abundance cannot be increased by more than 36% before the model predicts an infeasible outcome (*i.e.* there is no single solution that satisfies all the constraints within the model, Hazell and Norton, 1986). Interestingly, the model predicts that crofters should incorporate moorland grazing into their management regimes even without the constraint on bumblebee abundance, in contrast to actual behaviour. By utilising an additional 4.6 ha of moorland crofters would be able to increase cattle production by 35%, and increase their total revenue by 7% (Table 6.3). An indirect consequence of this change in land management is a 19% increase in bumblebee densities on the inbye to 9.9 bees ha⁻¹ of croft land. As no constraint is imposed in this instance the marginal cost is zero. However, increasing bumblebee densities beyond 9.9 bees ha⁻¹ of croft land leads to a reduction in overall gross margins compared to the unconstrained MG scenario and generates an opportunity cost of £78.

Interestingly, if crofters in mixed livestock systems are given the choice between the two management options, the models predict that they will only implement moorland grazing if the constraint on bumblebee density is ≤ 12.6 bees ha⁻¹ of croft land, at which point the availability of moorland grazing becomes a limiting factor. Above this threshold both moorland grazing and a wildflower mix are utilised. However, this has a significant impact on overall croft gross margins, which decrease by 35%, when compared to the optimal model, to achieve 12.7 bees ha⁻¹ of croft land.

Table 6.3. The percentage change in revenue, costs and land use under the two scenarios. Moorland Grazing is only applicable to the mixed livestock crofts on the Uists and the results are associated with a 30% increase in bumblebee densities. The Wildflower Mix scenario was examined for both systems. The results are also associated with a 30% increase in bumblebees (equivalent to 9.9 bees ha⁻¹). Shown as percentage change in relation to the optimal baseline model.

	Baseline	Uists		Lewis
		Moorland Grazing	Wildflower Mix – Mixed Crofts	Wildflower Mix – Sheep crofts
Croft Gross Margins	100	11	-4	-4
Total Revenue	100	7	0	-6
Total Variable Costs	100	3	-10	-10
Cattle numbers	100	35	-2	-
Cattle Revenue	100	34	-1	-
Cattle Variable Costs	100	33	-1	-
Sheep numbers	100	0	0	-13
Sheep Revenue	100	0	0	-11
Sheep Variable Costs	100	0	0	-10
Total Land Used	100	62	10	0
Area Inbye Grazing	100	-77	0	-20
Area Fallow	100	41	35	-
Area Silage	100	41	0	-

Figs. 6.1a-b. The impact of tightening the constraint on bumblebee abundance on croft gross margins for mixed livestock systems on the Uists (Fig. 6.1a) and sheep production systems on Lewis (Fig. 6.1b). Gross margins are shown in £/ha and the constraints on bumblebees are shown as the density of bumblebees per ha of croft land.



6.5. Discussion

6.5.1. The trade-off between bumblebee abundance and agriculture

Improving the ecological quality of agricultural land often requires a change to current land management practices and results in an opportunity cost to the agent (*i.e.* farmer or landowner) implementing the desired form of environmental management. Consequently, compensation is usually required. Within the EU this is primarily carried out through Agri-Environment Schemes (AES; *e.g.* Environmental Stewardship in England, Rural Priorities in Scotland) which reward farmers for employing environmentally sensitive farming methods. Interestingly, however, the results of our study suggest that in some instances compensation payments may not be required and that farming with a more environmental focus could generate economic, as well as environmental, benefits. In the crofting areas of northwest Scotland summer grazing by livestock on inbye land has been identified as a particular problem for foraging bumblebees and removing livestock from these areas has been suggested as an appropriate form of conservation management (Chapter 2). Relocating livestock to moorland grazings in summer is a traditional land management method that could be re-employed to achieve this desired environmental outcome. Re-grazing the moorland would require a change in land management on mixed livestock crofts; however, our models predict that this scenario would actually be more profitable than current crofting practices. Thus, by modifying their management regimes crofters operating in this system would increase their profits whilst providing an environmental good. That crofters do not engage in this practice suggests that they are not operating on the basis of pure profit maximisation, or that there are other constraints on their choice of management not captured by the model (such as the increasing age of crofters making the use of summer grazing unappealing). In my survey the majority of crofters who did not utilise the moorland grazings did so due to their age, and consequent difficulty in moving livestock between the inbye and hill (Chapter 5).

The availability and abundance of key foraging resources throughout the flight season are important factors for maintaining bumblebee populations in agricultural landscapes (Bäckman and Tiainen, 2002; Westphal *et al.*, 2006; Goulson *et al.*, 2008a). Sowing wildflower seed mixes at field margins is considered an effective means of increasing the abundance of suitable bumblebee flowers in intensively farmed areas (*e.g.* Carvell *et al.*, 2004; Pywell, *et al.*, 2005), and the inclusion of wildflower mixes into croft management has also been shown to be of value in what has traditionally been seen as a low intensity agricultural system (Chapter 2). However, these studies have not examined the financial implications to the farmer of introducing wildflower mixes into farm management practices. I show that the costs of utilising a wildflower mix vary with the type of farming system in operation. Introducing this method to mixed systems in marginal areas is relatively expensive, particularly with respect to the initial capital costs of habitat creation. These costs may make the use of this management tool somewhat prohibitive in such marginal farming systems, especially when less expensive options (*e.g.* moorland grazing) could be used. However, in sheep based systems the costs of introducing wildflower mixes as part of an AES are considerably less and may provide a more efficient means of increasing bumblebee populations as suitable foraging resources are scarce in this crofting system (Chapter 2). The density of foraging bumblebees utilising an introduced patch is thought to be determined by landscape context rather than patch size, with greater bumblebee densities on patches in more intensively managed agricultural landscapes with a lack of available foraging resources in adjacent semi-natural habitats (Heard *et al.*, 2007). Therefore, the addition of a small area of bumblebee specific wildflowers to sheep-only crofts could make a significant impact on bumblebee populations, with as little as 0.4 ha of wildflowers having the potential to increase bumblebees densities from an average of zero to 40 bees croft⁻¹ (equivalent to 5 bees ha⁻¹ of croft land). Although different bumblebee species have different sized foraging ranges (Knight *et al.*, 2005), the combination of small

unit size and the close proximity of sheep-only crofts to one another suggests that even a relatively low uptake of this approach would provide accessible patches for bumblebees with both long and short foraging ranges.

6.5.2. Considerations for developing agri-environmental payment schemes for bumblebee conservation

Following the Common Agricultural Policy (CAP) Reform in 2005 the calculation of compensation payments for farmers delivering public environmental goods has moved from an incentive based scheme to one of compensation for the losses incurred in meeting the requirements of agri-environment scheme prescriptions (Mettepenningen *et al.*, 2009). Income forgone through scheme participation is an important factor in this calculation, and has been estimated to account for 56% of total AES scheme costs (Mettepenningen *et al.*, 2009). In addition, the transaction costs associated with scheme uptake (*e.g.* the costs of farm conservation surveys or costs of legal advice) often impose a significant cost to the farmer, with estimates ranging from a conservative 5% of the total compensation payment to 25% (Falconer 2000; Mettepenningen *et al.*, 2009). Transaction costs are costs incurred by both the farmer (private transaction costs) and the public agency administering the AES in establishing, implementing or monitoring the agreements (public transaction costs). Private transaction costs may significantly affect a farmer's decision to participate in an AES and ultimately influence the success of a scheme (Vanslebrouck *et al.*, 2002). Such costs may be particularly prohibitive for farmers operating small businesses (Falconer, 2000). This is highly relevant to crofting, where income from agriculture often makes a small contribution to total household income. Indeed, transaction costs (either perceived or actual) were often considered as particular obstacles to participating in the latest Scottish AES by crofters managing small agricultural units on Harris and Lewis (Chapter 5). As highlighted by Falconer (2000), this is worrying as small farms are generally more likely to

support high biodiversity. Again, this is highly relevant to crofting due to the association of many rare species with crofted landscapes, *e.g.* the northern colletes bee (*Colletes floralis*), belted beauty moth (*Lycia zonaria*), and slender naiad (*Najas flexilis*).

The ecological impacts of altering current management practices also need to be considered in the creation of any future AES. For example, prior to reintroducing livestock to moorland areas an assessment of the current ecological state of the habitat would be required since heather moorlands are low productivity systems that are easily damaged by inappropriate grazing regimes (Thompson *et al.*, 1995). Overgrazing, in particular, can alter the vegetation structure and composition away from dwarf shrubs to graminoid species (Alonso *et al.*, 2001). Similarly, introducing non-native wildflowers to the machair system could have detrimental effects on the genetic composition of the local flora, thus sourcing of native seeds is essential.

The intensification of accessible lowland grasslands and the subsequent abandonment of relatively inaccessible grazings, such as moorlands, is a feature of crofting that has also been reported in other low intensity grazing systems in Fennoscandia, and the Swiss and Bavarian Alps (Caballero, 2007). Similarly, rural depopulation and the lack of interest from the younger generation in continuing in these traditionally labour intensive farming systems has been highlighted as a common social factor threatening their future across Europe (Caballero, 2007). Much of Europe's High Nature Value (HNV) farmland is found in these Less Favoured Areas (LFA), which account for 56% of the EU's total land mass (Caballero, 2007). These regions receive limited investment due to environmental and social constraints and, worryingly, studies at the European level suggest that current support schemes under the CAP are often not suitable for maintaining human populations in these areas (Caballero, 2007). Policies are required that take into account the social

fragility that is common in these areas, and how cultural heritage influences the management of the farming system (Caballero, 2007). The influence of cultural factors is evident to some extent in this study in that the majority of crofters managing mixed crofts persisted with sheep production even though our model shows this to be an unprofitable activity. In most instances sheep had been reared by the family over several generations, and current crofters continue with sheep production in keeping with tradition.

6.5.3. Conclusions

Ecological-economic modelling can be usefully employed to examine the trade-offs between socio-economic factors and environmental outcomes for a diverse range of systems. In this chapter I use LP based ecological-economic models to show that the cost-effectiveness of two bumblebee conservation measures in the Outer Hebrides varies according to the crofting system in operation and the intended method of conservation management. Since current land-use deviates from profit-maximising management, I compare optimal land-use with and without constraints on bumblebee abundance. Promoting the use of traditional summer moorland grazing practices in the mixed crofting systems found in the Uists and Harris would generate a net gain in income from crofting activities and would deliver greater bumblebee abundances on crofts without the need for compensation. Consequently, rather than investing in a traditional AES that may be limited by the associated transaction costs (real or perceived), policy-makers should consider investing in greater advocacy of environmentally beneficial management that also boosts croft income. In contrast, some form of payment based scheme is required to increase bumblebees on sheep production crofts found in Lewis. Although the payment rate required is relatively low, agricultural income and unit size is typically very small in this system and transaction costs are likely to be disproportionate to the compensation required. It is essential that policy-makers take this into consideration during the policy

design process. Social and cultural factors are also important in shaping land management practices in low intensity farming systems in LFAs, and must also be taken into account when developing agri-environmental policies for these unique areas of the EU.

Appendix II – The impacts of agricultural policy and market forces on croft economics

In addition to the data present in Chapter 6 I also examined the impacts of removing financial support through grants and AES on croft economics, as well as market forces. As the main impacts in both cases were mostly limited to changes in croft income rather than land management, this data was not included in the paper which forms the basis of this chapter. Therefore the data is presented as an appendix, to provide further insight into the economics of crofting in the Outer Hebrides.

a) Agricultural policy

Direct payments make a substantial contribution to croft income (>58%) in the Outer Hebrides. However, agricultural policy is currently in a state of flux and the future of such payments are uncertain. The loss of the SFP in 2013, and what may replace this scheme, is of particular interest to farmers and landowners. Therefore, in addition to the data presented in Chapter 6, I also examined the impact of losing the SFP on the gross margins and land management practices used in both models, and also how any changes in land management would affect the bumblebee populations supported by these activities. I also examined the impacts of losing the LFASS payment. In addition, the majority of crofters on the Uists received payments through AES agreements and under the Scottish Beef Calf Scheme (SBCS), therefore I also modelled the effects of removing these payments.

The decoupling of subsidies from production in 2005 has limited the impact of removing direct payments to loss of income and leaves land management practices unaffected. The SFP makes the largest contribution to croft income of all the subsidies received in the Outer Hebrides, therefore its loss is predicted to have the greatest financial impact on both

croft types (Table IIa). The LFASS is an important source of income to crofters managing sheep crofts and accounts for 42% of croft revenue. Consequently, removing this payment is also predicted to have a large negative impact on croft income in this system. In contrast, LFASS payments account for less than 20% of the total subsidies received on mixed livestock crofts. Interestingly, AES payments are of greater importance for this croft type and contribute to 34% of all subsidies received. The loss of these subsidies is predicted to reduce gross margins by 24% and income by 33%. Due to the constraints imposed on land management by agri-environment agreements the loss of these payments are also predicted to alter land use, reducing the area of abandoned land and increasing areas of silage and fallow, and therefore cattle production (Table IIa). Loss of the SBCS reduces the revenue from beef cattle production although cattle stocking rates remain unchanged. Cattle numbers are predicted to decline only if the market price of store calves plummets to less than 60% of the average return received during the reference period.

Table IIa. The impacts of losing agricultural payments on crofting in the Outer Hebrides.

Data shown as percent change compared to the baseline model.

	Baseline	No SFP	No LFASS	No AES
<i>Mixed Livestock Crofts</i>				
Gross margins	100	-38	-14	-24
Revenue	100	-29	-11	-17
Variable Costs	100	0	0	9
Subsidies	100	-48	-18	-34
Cattle nos.	100	0	0	10
Sheep nos.	100	0	0	0
Abandoned land	100	0	0	-50
Fallow	100	0	0	10
Silage	100	0	0	10
Ungrazed land	100	0	0	0
<i>Sheep Crofts</i>				
Gross margins	100	-51	-38	-
Revenue	100	-25	-19	-
Variable Costs	100	0	0	-
Subsidies	100	-58	-42	-

b) Market Forces

The effect of increasing market prices on the main inputs and outputs for each crofting system were examined in relation to croft income, management and the associated bumblebee populations. The inputs examined were NPK, cattle and sheep concentrates, and the outputs studied were the price of store calves and lambs. The effects of changing market prices differed between crofting systems. Increasing input prices were predicted to reduce croft income but have no effect on management practices on mixed livestock crofts whilst, in contrast, models predicted that a 25% increase in sheep concentrate prices would result in an 86% reduction in sheep numbers on sheep only crofts. Conversely, increasing output prices had no effect on sheep stocking rates. Altering the market value of cattle had no impact on levels of production, although cattle numbers always remained above zero due to crofters receiving the SBCS subsidy. An increase of 17% in store lamb prices was required for sheep to re-enter the mixed livestock model.

Chapter 7. Discussion

Agricultural intensification during the twentieth century has led to population declines in a range of farmland taxa throughout the UK and western Europe (Robinson and Sutherland, 2002). Bumblebees are no exception, with two extinctions and severe population declines experienced by at least six species in the UK in the last 60 years (Benton, 2006). Although considered habitat generalists (Goulson *et al.*, 2006), many of the UK's rare bumblebee species are now associated with marginal agricultural systems, such as crofting, which have not experienced the impacts of agricultural intensification to the same extent as elsewhere in the UK (Goulson *et al.*, 2006). As with the conservation of many organisms worldwide, the persistence of bumblebees in these marginal areas is strongly associated with the local communities who are responsible for land management in the region. Consequently, the survival of several of the UK's rarest bumblebee species is inextricably linked with the future of the crofting communities found in northwest Scotland. However, the nature of crofting is changing, with methods becoming more intensive and the simplification of practices becoming increasingly common. As a result, future conservation management aimed at bumblebees in crofting areas cannot be addressed without first examining the socio-economic drivers of change within crofting communities.

The aim of my research was therefore to examine the economic processes required to support crofting communities in the use of environmentally beneficial land management practices and, in turn, determine the economic cost of conserving the endangered bumblebee fauna dependant on crofted land. In this chapter I review the findings of my research and discuss them in relation to the existing body of literature. I also look back over my project to evaluate areas which I feel have been particularly successful, discuss any limitations I have found and identify the potential for further work.

7.1. Habitat use by foraging bumblebees in agricultural landscapes

Low intensity agricultural systems, such as the crofting systems of northwest Scotland, are often considered to be of greater benefit to farmland biodiversity than more intensively managed systems. Low intensity grazing systems are often characterised by their small scale and the rotational nature of the arable and grazing activities undertaken. Consequently, these systems can promote a mosaic of habitat types within the agricultural landscape, and this diversity of habitats is an essential landscape feature known to promote bumblebee abundance and diversity (Charman, 2007; Rundlöf *et al.*, 2008), in addition to species richness for a variety of other taxa (Weibull *et al.*, 2003). As such, crofted land is of significant ecological interest, both nationally and internationally. Traditional crofting practices provide habitats for some of the UK's rarest fauna, including *B. distinguendus* and *B. muscorum*, two of the UK's rarest bumblebee species. In addition, machair based crofting systems provide some of the last remaining refuges in the UK for a wealth of biodiversity, including other invertebrates (*e.g.* northern colletes bee [*Colletes floralis*] and belted beauty moth [*Lycia zonaria*]), birds (*e.g.* corncrake [*Crex crex*]), and plants (slender naiad [*Najas flexilis*]; Love, 2003). However, the data I present in Chapters 2 and 3 demonstrates that current croft land management practices do not support high abundances of these rare bumblebees or their forage plants. Indeed, in a much earlier study Mänd *et al.* (2002) highlight that even in the heterogeneous low intensity agricultural systems in operation in Estonia, bumblebee diversity was greatest in adjacent off-farm habitats.

Crofting is currently undergoing a period of intensification; simplification of agricultural practices is increasingly common resulting in the loss of landscape heterogeneity. A move towards intensive sheep production on the inbye is creating significant overgrazing problems (Willis, 1991). This is exemplified by the data presented in Chapter 2, which shows that significantly more bumblebees were recorded foraging in areas where sheep

grazing was absent. Even at low stocking densities the presence of sheep had a detrimental impact on the availability of bumblebee forage plants on inbye grazings. The level of sheep grazing during the summer is therefore an important determinant of the ecological value of crofts to foraging bumblebees. The impacts of cattle grazing on bumblebee populations in crofted areas could not be analysed in isolation as cattle were only present within a mixed grazed system. However, extensive cattle grazing forms the predominant grazing regime implemented by farmers in the southwest of England, and the results presented in Chapter 3 highlight the value of this management practice to short-tongued bumblebees on the Somerset Levels. Carvell (2002) also identified cattle grazing regimes as a beneficial land management tool for promoting bumblebee abundance in grassland systems in southern England, and highlighted the importance of extensive cattle grazing between April and September. In my study this grazing regime provided a wealth of forage plants throughout early – mid summer, particularly stands of white clover. However, this species flowers early in the season and in the cattle grazed pastures of the Somerset Levels, no other key forage plant succeeded this species. The availability and abundance of key bumblebee forage plants throughout the flight season are crucial for maintaining diverse bumblebee assemblages (Bäckman and Tiainen, 2002; Westphal *et al.*, 2006; Goulson *et al.*, 2008b), therefore additional sources of forage are required in late summer to support the final stages of colony development in these areas.

The intensification of crofting practices is driving the loss of key bumblebee forage plant species from the crofted landscape, therefore the value of adjacent non-agricultural habitats, such as road verges and track edges, are increasingly important as sources of additional forage. Road verges located along rural road networks may provide important habitats for farmland biodiversity (Pauwels and Gulinck, 2000), and have the potential to benefit a range of invertebrates (*e.g.* Saarinen *et al.*, 2005; Noordijk *et al.*, 2009). If

managed appropriately there is evidence to suggest that these non-agricultural habitats may increase the abundance and diversity of bumblebee populations, particularly in intensively managed agricultural landscapes (Hopwood, 2008). Both road verges and track edges provided important foraging habitats for long-tongued bumblebee species in both farming systems I examined (Chapter 3). The changing nature of crofting also suggests that more emphasis needs to be placed on these habitats as part of future conservation measures for providing bumblebee habitats within this region.

The use of floral resources by foraging bumblebees in my study reflects the findings of previous authors (*e.g.* Goulson and Darvill, 2004). A large proportion of foraging visits made by bumblebees in both agricultural systems I examined were made to a small number of the available forage plants, suggesting that the abundance of bumblebees is related to the availability of a few key forage plant species rather than particularly diverse floral assemblages. Members of the Fabaceae and Asteraceae made up a significant proportion of foraging visits, and wildflower 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 and Tiainen, 2002; Goulson and Darvill, 2004; Goulson *et al.*, 2005; Carvell *et al.*, 2006; Diekötter *et al.*, 2006). Several studies have helped to identify which conservation seed mixes are most useful for foraging bumblebees (*e.g.* Carvell *et al.*, 2007), although much of the research has focused on intensive lowland farms in England (Pywell *et al.*, 2004; Pywell *et al.*, 2006; Carvell *et al.*, 2007). In crofted areas red clover was most abundant in sections sown with a ‘bird and bumblebee’ conservation seed mix, and the strong association between bumblebees and this management type suggests that Fabaceae-rich mixes would also be highly appropriate within the context of bumblebee conservation in northwest Scotland.

7.2. Considerations for developing Agri-Environment Schemes for conserving bumblebees in marginal areas

The marginal agricultural regions of the EU are typically complex areas whose characteristics are defined by a range of socio-economic and environmental constraints. Due to their remote nature they are often located within Less Favoured Areas (LFAs). Low intensity agriculture, particularly traditional grazing systems, characterise the farming practices in these regions (Caballero, 2007). However, rural depopulation and the lack of interest from younger generations in continuing in these traditionally labour intensive farming systems is a common social factor threatening the future of marginal areas across the whole of Europe (Caballero, 2007). In addition, agricultural land in marginal areas is often of high ecological importance, with much of the EU's High Nature Value (HNV) farmland found in LFAs (Caballera, 2007). This combination of social factors coupled with a difficult environment has led to the intensification of accessible lowland grasslands and the subsequent abandonment of relatively inaccessible grazings, such as moorlands, in several LFAs in Europe (Caballero, 2007). As the data presented in Chapter 5 demonstrates, crofting in northwest Scotland is no exception, with rural crofting communities facing similar social and ecological issues as communities in other LFAs elsewhere in the EU.

Large swathes of croft land are designated as Special Areas of Conservation (SACs) and Special Protection Areas (SPAs) at the EU level, and as Sites of Special Scientific Interest (SSSI) at the national level in recognition of their high ecological value. However, as these areas have not been designated specifically for bumblebees, the land management practices implemented within them will not necessarily be of benefit to this taxonomic group. As in other LFAs, the persistence of the diverse ecological communities that have developed in crofted areas relies upon the continuation of traditional agricultural practices,

in this instance crofting. However, as the data in Chapter 5 highlights, crofting is experiencing a period of significant social change: the demographic structure of crofting communities, particularly in the Outer Hebrides, is evolving in response to a range of socio-economic factors, and subsequently altering the how croft land is currently managed. Although there are numerous factors driving these changes, it would appear that there are three principal causes: a) an aging crofting population; b) out-migration of younger generations; c) in-migration from the mainland. I consider each factor in turn below:

a) An aging population

The average age of active crofters (*i.e.* crofters who actively manage their land for agricultural purposes) is increasing and is particularly apparent in the Outer Hebrides where a 10% increase in the number of people aged between 55 - 59 was experienced between 2003 and 2005, during which time the number of children aged under 15 continued to decline (Hall Aitken, 2007). In addition, it is predicted that 33% of the region's population will be over the age of 65 by 2031 (Comhairle nan Eilean Siar, 2009a,b). Indeed, the majority of crofters I interviewed for this project were over the age of 65. In addition to the social and economic problems associated with a predominantly elderly population, the changing demographic structure of crofting communities also has serious ramifications for the natural environment. For example, the traditional practice of handing down the management of the croft from one generation to the next is not as common as it once was, resulting either in the complete abandonment of the land or the amalgamation of crofts. Both scenarios have a negative outcome for biodiversity: the abandonment of croft land allows rushes to colonise and results in the ecological degradation of the land (Crofters Commission, 1991), whilst amalgamating the management of one croft with that of several others may promote the loss of landscape diversity from crofted areas.

Crofting practices have become steadily more intensive, particularly with respect to sheep production, and this has resulted in a change to traditional grazing practices. Traditionally, sheep were moved to common moorland grazings during the summer months and crofters with shares in sheep stock clubs would employ a shepherd to tend the animals as one flock (Hance, 1952; Willis, 1991). However, the role of the community shepherd has disappeared from most crofting areas as it is too expensive to maintain, and the onus has now shifted to the individual crofter to move and gather his own flocks. Following this change in responsibility, the practice has now declined and has led to an increase in year round grazing of the inbye (Willis, 1991). This trend is currently being exacerbated by the increased age and subsequent reduced physical ability of crofters.

Elderly crofters find sheep production less labour intensive than beef production. Although less profitable than rearing cattle, the agricultural inputs required for sheep production are fewer, and the ability to intensively graze the inbye rather than move livestock to the hill means crofters are often able to manage livestock without requiring additional help from contractors. As I have shown in Chapter 2, sheep grazing on inbye land has a particularly detrimental impact on the availability of bumblebee forage plants, and results in the absence of bumblebees from sheep grazed pastures. Therefore, the continuation of this more intensive form of management, particularly in the Outer Hebrides, has significant ecological consequences.

b) Out-migration

The population of the Outer Hebrides has been declining since the early twentieth century, with a 43% reduction in total population between 1901 and 2001 (Hall Aitken, 2007). The population of this region is still changing, with an 8.5% decrease in total population experienced between 1995 and 2005 (Hall Aitken, 2007). A small increase of 1% has been

recorded since 2003, however out-migration is still an observed trend, particularly amongst the younger generations and women (Hall Aitken, 2007). Amongst the variety of socio-economic factors driving this decline, the nature of crofting is one of them: crofting is a labour intensive and relatively unprofitable activity, where the majority of crofters require additional sources of household income to support themselves and their families. Consequently, as in many other LFAs throughout the EU (Caballero, 2007), younger people are not interested in continuing in such a difficult and unprofitable agricultural industry.

The Outer Hebrides also suffer from a lack of skilled jobs, with primary sectors, such as crofting and fishing, forming the main source of employment. The unemployment rate is therefore increasing and is one of the highest in the region, rising to 2% above the rate recorded for the Highlands and Islands Enterprise (HIE) area between January 2001 and August 2003 (HIE, 2003). Consequently, many young people are leaving the region to forge careers on the mainland. In addition, the educational aspirations of islanders are also driving the loss of younger generations from the Outer Hebrides. With limited opportunities for further education in the region, many students choose to study at colleges and universities on the mainland (Hall Aitken, 2007). The supply of affordable housing is another driver of emigration from the Outer Hebrides. Increased demand for housing due to the in-migration of people from the mainland, has driven up house prices to such a level that this is now a critical issue for local people returning from university (Hall Aitken, 2007).

As a result of out-migration, the population structure of the Outer Hebrides is becoming biased towards an elderly and predominantly male population (Hall Aitken, 2007; Mackenzie, 2007; Comhairle nan Eilean Siar, 2009a,b). The subsequent reduction in

crofters actively managing the land will, again, result in the use of more intensive land management practices to make agricultural activities more efficient and economically viable, and therefore reduce the ecological value of croft land.

c) In-migration

In-migration is experienced throughout the Crofting Counties and takes several forms. Often the flow of migrants to the region is characterised by middle class families or older age groups (>45 years old) who have little agricultural experience but are seeking a 'better life' in the region (Willis, 2001; Hall Aitken, 2007). These 'lifestyle immigrants' tend to purchase property in remote, scenic areas and are partially responsible for the sharp increase in house prices experienced in the region. Another faction of immigrants, particularly in the Outer Hebrides, is comprised of economic migrants from foreign countries who have migrated to address labour shortages for unskilled workers in non-agricultural industries (Hall Aitken, 2007). The emergence of short stay professionals forms another group of immigrants to the region (Hall Aitken, 2007). However, by definition this group are not permanent residents and often have families living elsewhere, therefore adding little to communities.

As immigrants often work in non-agricultural roles the risk of land abandonment increases. Although the 'lifestyle immigrants' may endeavour to undertake some form of agricultural activity on their land, they often have little practical farming experience, which does little to preserve traditional crofting practices.

As socio-economic factors are so influential in marginal areas, they form a particularly important consideration in the development of agri-environmental schemes (AES) when using a mathematical programming approach, as I have done in Chapter 6. As social

factors are exogenous to programming models, non-economic aspects of agent behaviour are not taken into account in the modelling process. Cultural heritage is at the centre of crofting, therefore crofters make decisions based on criteria other than pure profit maximisation. As this is not taken into consideration by the model in the calculation of the optimal production plan, discrepancies may arise between model predictions and real world occurrences. This is evident in my study which shows that the majority of crofters managing mixed crofts persisted with sheep production even though the activity was absent from the optimal production plan. In most instances crofters continued with sheep production in keeping with family tradition. Consequently, a good understanding of the mechanisms driving changes in rural communities, and how these in turn influence current land-use is essential for the success of future conservation initiatives in marginal areas.

AES are the primary mechanisms through which agricultural policies meet their environmental objectives, and are common throughout Europe. Under the CAP, EU member states are required to develop their own AES programmes, and in Scotland the 'Rural Priorities' scheme is available to crofters under the current Scottish Rural Development Programme (SRDP) 2007 – 2013. The success of such AES relies on the willingness of farmers to voluntarily participate in schemes. However, improving the quality of agricultural land for biodiversity conservation often requires a change in land-use and incurs an opportunity cost to the agent implementing the desired form of management. The opportunity costs to the agent are formed by the forgoing of another activity that could take place on the land enrolled in the AES, therefore compensation is usually required. Compensation payments are principally calculated from the income forgone through scheme participation, and are estimated to account for 56% of total AES scheme costs (Mettepenningen *et al.*, 2009). However, transaction costs (*e.g.* the costs of farm conservation surveys or costs of legal advice) are also associated with AES uptake

and can impose a significant cost to the farmer participating within a scheme, with estimates ranging from 5% of the total compensation payment to 25% (Falconer 2000; Mettepenningen *et al.*, 2009). The private transaction costs incurred by farmers may significantly influence whether they participate in an AES, and subsequently influence the overall scheme success (Vanslebrouck *et al.*, 2002). In Scotland, the Rural Priorities scheme is open to all land managers throughout the country and does not take into consideration the marginal nature of crofting. As it is a competitive scheme, it is particularly difficult for crofters to compete with the larger farm businesses in the rest of Scotland, as they do not have the ability to absorb such costs (Falconer 2000). Indeed, private transaction costs (either real or perceived) were the most commonly cited reason for crofters not participating in current/future AES in my study. The administrative burden of the application process, including the requirement to apply online, and the negligible perceived benefits of the scheme were specifically highlighted as barriers to scheme participation. Therefore, a simplified application process and competition for agreements limited to the Crofting Counties would improve the crofter's chances of acceptance into a scheme and boost confidence in AES on the whole. A new scheme specific to crofting, which benefits and appeals to the rural communities responsible for land management, as well as conservationists, urgently needs to be developed in order to be included in the forthcoming rural development plan in 2013.

At present, there are no prescriptions available under the SRDP specifically aimed at bumblebee conservation, despite the distribution of two of the UK's rarest species being restricted to northwest Scotland. Therefore, any future AES developed for the crofted areas of the Outer Hebrides and the Crofting Counties should address the conservation needs of these endangered insects. In Chapter 6 I demonstrate that a 'one size fits all' management prescription is not suitable for bumblebee conservation in these marginal

systems, as the cost-effectiveness of bumblebee conservation (*i.e.* the maximum conservation gain for minimum economic cost) appears to vary depending on the type of crofting undertaken. In sheep based systems the introduction of a wildflower mix appears to be the most cost-effective means of increasing bumblebee abundance on crofts where bumblebee forage plants are extremely scarce. Although different bumblebee species have different sized foraging ranges (Knight *et al.*, 2005), the combination of small unit size and the close proximity of sheep-only crofts to one another suggests that even a relatively low uptake of this approach would provide accessible patches for bumblebees with both long and short foraging ranges.

However, this method does not provide a cost-effective means of increasing bumblebee densities on mixed livestock crofts. In some instances the use of AES may not be the most appropriate means of achieving environmental objectives (although this is subject to several caveats). Certainly on the mixed crofts typical of the Uists and Harris bumblebee abundance and the gross margins associated with all crofting activities were greatest in the unconstrained model, where crofters introduced moorland grazing to their management regimes during the summer months. As crofting in a more environmentally sensitive manner generates both ecological and economic gains under this scenario, the need for compensation payments, and therefore an AES, would be negated. This suggests that investment in advocacy work is a more appropriate and cost-effective allocation of funds in this situation. However, despite the financial gain crofters would receive if they were to modify their current land management practices, the fact that they do not currently engage in this management practice suggests that they are not operating on the basis of pure profit maximisation, and that other factors exogenous to the model are influencing management decisions. As discussed previously, the strong influence of socio-economic factors on crofter behaviour must be taken into account in conservation management in marginal

agricultural systems. For example, reintroducing moorland grazing would be a realistic solution to conserving bumblebees within rural communities with a natural aversion to AES, as is demonstrated by many crofters. No formal agreement would need to be entered, therefore the transaction costs which are so prohibitive to scheme participation would be absent. However, the increasing age of crofters and consequent difficulty in moving livestock between the inbye and hill suggests that reintroducing this practice would be an unappealing prospect to many and receive limited uptake under current social conditions.

7.3. Management recommendations for bumblebee conservation

The conservation of bumblebees relies on the presence of a heterogeneous landscape that provides a mosaic of suitable habitats in which bumblebees may fulfil their life cycles. In this study I have focused my attentions upon the provision of suitable foraging habitats, although the availability of suitable nesting and hibernation sites are also important aspects of bumblebee conservation. In relation to foraging habitats, there are three key elements that need consideration to successfully conserve bumblebees in agricultural landscapes: a) grazing management; b) non-agricultural habitats; and, c) forage. I discuss each in turn below:

a) Grazing management

Grazing forms an integral part of the agricultural systems I examined during this study, and grazing management plays an important role in promoting the abundance and diversity of floral resources within farmed landscapes. As grazing systems are so varied throughout the UK, the type and intensity of production of the farming system in use needs to be taken into consideration when developing grazing management prescriptions specifically aimed at bumblebee conservation.

In the mixed livestock crofting systems typical of the Outer Hebrides, land grazed by sheep or a combination of cattle or sheep have a detrimental impact on the abundance of key bumblebee forage plants and therefore bumblebees. In contrast, land which was not grazed continuously throughout the summer, such as winter grazed pasture often supports more floristically diverse and abundant assemblages of bumblebee forage plants, and reflects a traditional form of grazing management. In addition, utilising moorland grazings also provides a financial gain for crofters. Therefore, I would strongly recommend a return to the traditional practice of relocating livestock to hill grazings during the summer months where possible. In instances where this practice cannot be implemented (*i.e.* due to old age) an alternative possibility may be to increase grazing densities on some parts of the croft, thereby allowing others to be left ungrazed on a rotational basis. In both instances, funding available through Pillar II of the CAP should be invested in developing advocacy programmes in which support and advice are freely available to crofters. This could also provide an opportunity to educate ‘lifestyle immigrants’ in traditional crofting practices, reinstate moorland grazing regimes and therefore support the continuation of traditional low intensity crofting in the region. In a region where AES are perceived with such negativity, investing in advisory officer positions may be a more efficient allocation of funding and produce more effective results.

In the extensively grazed beef production systems of southwest England there is scope to increase the abundance of floral resources in late summer. This could be achieved through the creation of wildflower rich margins (available under the Higher Level Stewardship Scheme in England) in silage fields or through the use of a similar wildflower mix prescription suggested for sheep based crofting systems.

b) Non-agricultural habitats

Non-agricultural habitats, such as road verges and track edges, may provide important additional sources of forage for bumblebees in agricultural landscapes throughout the UK and Europe where landscape heterogeneity is limited and floral resources are scarce. The responsibility for the management of road verges in the UK falls to local authorities, and any management undertaken needs to be sympathetic to the requirements of bumblebees and other invertebrates that utilise these habitats. Cutting of road verges was a common tool utilised in southwest England to manage these habitats. Cutting regimes should ensure forage remains available throughout the season and could be achieved simply by staggering the timing of the cut throughout an area to ensure some habitat always remains intact throughout the season. As road verges are found on non-agricultural land they fall outside the scope of AES payments to encourage the use of beneficial management practices. Therefore, I suggest that road verges are integrated into local authority land management and habitat action plans. In areas of intensive agricultural activity where floral resources are scarce and the nutritional requirements of bumblebees cannot be met, road verges which support high densities of key flowering plants should be considered of high conservation value and therefore receive some form of environmental protection. In addition, with the increasingly fragmented nature of many bumblebee populations, such as *B. sylvarum*, and the reintroduction of *B. subterraneus* to southeast England, the rural road network may also provide an important dispersal mechanism connecting suitable bumblebee habitats within the wider landscape. Therefore, it would be useful to determine whether road verges do, or have the potential to, act as ‘ecological corridors’ along which bumblebee populations could expand and colonise new areas.

c) Forage

The species composition and abundance of foraging resources are critical for maintaining the diversity of foraging bumblebees (Goulson *et al.*, 2008b). Sowing a wildflower seed mix can be an effective means of increasing bumblebee abundance in agricultural areas, and I would recommend this method as a cost-effective prescription for use in sheep based crofting systems. This study, and others (*e.g.* Goulson and Darvill, 2004), have shown that bumblebee abundance is associated with the availability of a few key forage plant species, therefore wildflower mixes aimed at conserving bumblebees on crofts should increase the availability of a narrow range of key plant species rather than maximise species diversity. Members of the Fabaceae appear to be particularly important to foraging bumblebees in agricultural landscapes, especially red and white clover (Bäckman and Tiainen, 2002; Goulson and Darvill, 2004; Goulson *et al.*, 2005; Carvell *et al.*, 2006; Diekötter *et al.*, 2006), therefore these species should form the principal components of any wildflower mix implemented. The provision of floral resources throughout the bumblebee's flight season is particularly important (Bäckman and Tiainen, 2002; Westphal *et al.*, 2006), even within low intensity agricultural systems (Mänd *et al.*, 2002). The inclusion of spring flowering species would also be of value to nest founding queen bumblebees (Lye *et al.*, 2009).

7.4. Conclusion

The persistence of farmland biodiversity in marginal areas is strongly associated with the future of the communities responsible for land-use in the region. This is particularly relevant to the persistence of the rare bumblebees associated with crofted landscapes. Crofting is undergoing significant social change and these changes are reflected in the land management practices utilised by crofters throughout northwest Scotland. Crofters are complex agents who are not solely motivated by profit maximisation, but also by cultural factors. That croft management decisions are not driven purely by economics is likely to

impact on the uptake of particular AES or conservation prescriptions and, on this basis, I would speculate that management reflecting a return to traditional crofting practices may be a more preferred conservation management option than introducing a new practice which has no cultural relevance. Consequently, an interdisciplinary approach which takes into consideration culture and the socio-economic drivers of community change, in conjunction with the ecological impacts of subsequent land-use change, is essential for developing effective conservation measures for any farmland biodiversity in marginal systems.

7.5. Evaluation of this research

The survival of two of the UK's rarest bumblebee species depends on the continuation of crofting in northern Scotland. However, crofting is a marginal agricultural system that is heavily influenced by the cultural heritage associated with the crofting way of life, and is extremely vulnerable to change. The close relationship that exists between the crofting community and the way in which croft land is managed has meant that in order to determine whether bumblebee conservation in this region could be reconciled with the continuation of a viable crofting system, an interdisciplinary approach was required. Undertaking an interdisciplinary approach to address this type of conservation problem is not uncommon, as it is now widely recognised that biodiversity conservation and the provision of environmental services depends on the communities responsible for implementing land management in the region. My research is therefore not novel in the sense that I have not utilised a ground breaking new technique or developed a new framework for conservation science. However, much research still focuses on either the conservation needs of a specific species or habitat, or the economic impact of modifying agent behaviour for the benefit of conservation. Although my study focuses on a particular taxon and agricultural system, the interdisciplinary approach I have employed is highly

flexible and may be applied to a wide variety of other conservation, or environmental, problems. Therefore, the value of my research lies in the contribution it makes to the increasing, but still relatively small, body of literature that utilises ecological-economic modelling to address conservation problems in an interdisciplinary manner.

The ecological outputs of this project make an important contribution to the knowledge base supporting bumblebee conservation efforts, particularly in the lesser studied crofting systems of northwest Scotland. The relationship between crofting and bumblebee abundance has not previously been quantified, with the assumption that crofting is beneficial for biodiversity, particularly rare bumblebees, generally accepted. However, my research has demonstrated that current croft management techniques do not support significant populations of these invertebrates, and has highlighted the need for conservation intervention if these rare populations are to persist in this region. In addition, my research into the use of non-agricultural habitats supports the findings of other studies (*e.g.* Mänd *et al.*, 2002; Saarinen *et al.*, 2005; Hopwood, 2008; Noordijk *et al.*, 2009) which highlight the importance of these habitats to foraging bumblebees and other invertebrates, thus raising the profile of these sometimes overlooked habitats.

Chapter 6, in which I develop ecological-economic models to explore the possible outcomes of bumblebee conservation measures on the economics of crofting, is the chapter in which the greatest limitations of my research are found, in the assumption of rational behaviour on the part of farmers by the modelling framework. In other agricultural systems this assumption may not be that far-fetched, with farmers' management decisions primarily driven by profit maximising behaviour. However, from examining crofting in more detail it is clear that croft management decisions are influenced by a range of factors, such as cultural heritage, that are exogenous to the models.

Addressing the influence of these socio-cultural factors (or ‘irrational behaviour’) on crofter behaviour is difficult, as LP models do not take these factors into consideration. However, in situations where a socio-cultural factor has a known outcome on land-use it may be possible to build a constraint into the model to reflect this. For example, elderly crofters do not utilise moorland grazings, therefore a constraint which effectively says ‘if over 60, then do not use moorland’ could be included to prevent moorland grazing being included as an activity in the optimal production plan. This seems the most sensible approach if feasible within a LP modelling framework. Agent-based models provide an alternative modelling approach which could possibly reduce the influence of exogenous factors, as agents within the model are able to influence and learn from one another. However, these models focus on macro-level responses to micro-level changes in agent behaviour, rather than the micro-level effects of change on agent behaviour, which was the focus of my study.

Another limitation to the ecological-economic models was the small sample size on which the models were based for each crofting system. Finding willing participants amongst the crofting community was incredibly difficult, therefore the sample size of my survey was limited to only 19 crofters throughout the entire study area. This has implications for the extent to which the models may apply to the systems they represent; a larger sample size would increase the robustness of the model calibration process. Similarly, now that I have a greater understanding of mathematical optimisation models and their data requirements, I would modify the crofter survey to incorporate an additional level of detail that would have enabled me to take the modelling process an additional stage further, and provide a greater insight into each crofting system.

Therefore, although the results of the ecological-economic modelling process are interesting and will, in some instances, be a useful guide to future conservation initiatives, in many cases their real world applications may be limited by these external factors.

Opportunities exist for further studies based on the research presented in this thesis. The flexible nature of the ecological-economic modelling approach utilised in this project may be extended to other taxa which rely on marginal farming systems in other LFAs of the EU, or to examine the relationships between bumblebees and farming in other agricultural systems, either within Europe or elsewhere in their global range.

References

- Acs, S., Hanley, N., Dallimer, M., Gaston, K.J., Robertson, P., Wilson, P., Armsworth, P.R., 2010. The effect of decoupling on marginal agricultural systems: Implications for farm incomes, land use and upland ecology. *Land Use Policy*. 27, 550-563.
- Alonso, I., Hartley, S.E., Thurlow, M., 2001. Competition between heather and grasses on Scottish moorlands: Interacting effects of nutrient enrichment and grazing regime. *Journal of Vegetation Science*. 12, 249-260.
- An, L., Linderman, M., Qi, Jianguo, Shortridge, A., Liu, J., 2005. Exploring Complexity in a Human-Environment System: An Agent-Based Spatial Model for Multidisciplinary and Multiscale Integration. *Annals of the Association of American Geographers*. 95, 54-79.
- Angus, S., 2001. The Outer Hebrides moor and machair. The White Horse Press, Cambridge.
- de Aranzabal, I., Schmitz, M.F., Aguilera, P., Pineda, F.D., 2008. Modelling of landscape changes derived from the dynamics of socio-ecological systems. A case of study in a semiarid Mediterranean landscape. *Ecological Indicators*. 8, 672-685.
- Bäckman, J-P.C., Tiainen, J., 2002. Habitat quality of field margins in a finish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). *Agriculture, Ecosystems & Environment*. 89, 53-68.
- Baer, B., Schmid-Hempel, P., 2003. Effects of selective episodes in the field on life history traits in the bumblebee *Bombus terrestris*. *OIKOS*. 101, 563-568.

- Banaszak, J., 1983. Ecology of bees (Apoidea) of agricultural landscape. *Polish Ecological Studies*. 9, 421–505.
- Barnard, C.S., Nix, J.S., 1980. Farm Planning and Control. 2nd Edition. Cambridge University Press.
- Bartolini, F., Bazzani, G.M., Gallerani, V., Raggi, M., Viaggi, D., 2007. The impact of water and agricultural policy scenarios on irrigated farming systems in Italy: An analysis based on farm level multi-attribute linear programming models. *Agricultural Systems*. 93, 90-114.
- Beaton, C., Catto, J., Kerr, G., 2007. The Farm Management Handbook 2007/08, Scottish Agricultural College, Edinburgh.
- Benton, T., 2006. Bumblebees – The natural history and identification of the species found in Britain, Harper Collins, London.
- Benton, T.G. and Foster, W.A., 1992. Altruistic housekeeping in a social aphid. *Proceedings of the Royal Society of London – Series B*. 247, 199-202.
- Berendse, F., Chamberlain, D., Kleijn, D. and Schekkerman, H., 2004. Declining biodiversity in agricultural landscapes and the effectiveness of Agri-environment Schemes. *Ambio*. 33, 499-502.
- Birdlife International, 2004. Birds in the European Union: a status assessment. Birdlife International. Wageningen, The Netherlands.

Brooks, R.J., Shi, D., 2006. The calibration of agent-based simulation models and their use for prediction. In: Proceedings of the 2006 OR Society Simulation Workshop. Eds: Robinson, S., Taylor, S., Brailsford, S., Garnett, J.

Caballero, R., 2007. High Nature Value (HNV) Grazing Systems in Europe: A Link between Biodiversity and Farm Economics. *The Open Agricultural Journal*. 1, 11-19.

Cain, P., Anwar, M., Rowlinson, P., 2007. Assessing the critical factors affecting the viability of small-scale dairy farms in the Punjab region of Pakistan to inform agricultural extension programmes. *Agricultural Systems*. 94, 320-330

Caird, J.B., 1979. Land use in the Uists since 1800. *Proceedings of the Royal Society of Edinburgh*. 77B, 505-526.

Caird, J.B., 1987. The creation of crofts and new settlement patterns in the Highlands and Islands of Scotland. *Scottish Geographical Magazine*. 103, 67-75.

Cameron, A.D., 1986. Go listen to the crofters: The Napier Commission and crofting a century ago. Acair, Stornoway.

Carpentier, C.L., Vosti, S.A., Witcover, J., 2000. Intensified production systems on western Brazilian Amazon settlement farms: could they save the forest? *Agriculture, Ecosystems and Environment*. 82, 73-88.

Carreck, N.L., Williams I.H., 2002. Food for insect pollinators on farmland: insect visits to flowers and annual seed mixtures. *Journal of Insect Conservation*. 6, 13-23.

Carvell, C., 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation*. 103, 33-49.

Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D., Goulson, D., 2006. Declines in the forage availability for bumblebees at a national scale. *Biological Conservation*. 132, 481-489.

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D., Nowakowski, M., 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*. 44, 29-40.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubbs, M., 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*. 37, 771-788.

Charman, T., 2007. Ecology and conservation genetics of *Bombus distinguendus*, the Great Yellow Bumblebee. PhD thesis, University of Cambridge.

Colla, S. R., Otterstatter, M.C., Gegear, R. J., Thomson, J. D., 2006. Plight of the bumble bee: Pathogen spillover from commercial to wild populations. *Biological Conservation*. 129, 461-467.

Comhairle nan Eilean Siar, 2009a. Factfile – Socio-economic Review. January 2009. Development Department. Available to view at: www.cne-siar.gov.uk/factfile/socioeconomicoverview.asp Accessed 7th May 2009.

Comhairle nan Eilean Siar, 2009b. Outer Hebrides Fact Card. April 2009. Available to view at: www.cne-siar.gov.uk/factfile/documents/OHFactCards.pdf Accessed on 11th May 2009.

Cooke, I.R., Queenborough, S.A., Mattison, E.H.A., Bailey, A.P., Sandars, D.L., Graves, A.R., Morris, J., Atkinson, P.W., Trawick, P., Freckleton, R.P., Watkinson, A.R., Sutherland, W.J., 2009. Integrating socio-economics and ecology: a taxonomy of quantitative methods and a review of their use in agro-ecology. *Journal of Applied Ecology*. 46, 269-277

Crofters Commission, 1991. Crofting in the '90s. The Crofters Commission, Inverness.

Croxton, P.J., Carvell, C., Mountford, J.O., Sparks, T.H., 2002. A comparison of green lanes and field margins as bumblebee habitat in an arable landscape. *Biological Conservation*. 107, 365-374.

Danforth, B.N., 2002. Evolution of sociality in a primitively eusocial lineage of bees. *PNAS*. 99: 286-290

Department of Farming and Rural Affairs (DEFRA), Agriculture in the United Kingdom, 2007. Statistics available at <https://statistics.defra.gov.uk/esg>. Accessed 20th March 2009.

Diekötter, T., Walther-Hellwig, K., Conradi, M., Suter, M. & Frankl, R., 2006. Effects of landscape elements on the distribution of the rare bumblebee species *Bombus muscorum* in an agricultural landscape. *Biodiversity and Conservation*. 15, 57-68.

Dogliotti, S., van Ittersum, M.K., Rossing, W.A.H., 2005. A method for exploring sustainable development options at farm scale: a case study for vegetable farms in South Uruguay. *Agricultural Systems*. 86, 29-51.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society London, B*. 268, 25-29.

Dorrrough, J., Vesk., P.A., Moll, J., 2008. Integrating ecological uncertainty and farm-scale economics when planning restoration. *Journal of Applied Ecology*. 45, 288-295.

Drechsler, M., Grimm, V., Myšiak., J., Wätzold, F., 2005. Differences and similarities between ecological and economic models. Discussion paper 5/2005. UFZ – Centre for Environmental Research. Leipzig, Germany.

Drechsler, M., Johst, K., Ohl, C., Wätzold, F., 2007a. Designing Cost-Effective Payments for Conservation Measures to Generate Spatiotemporal Habitat Heterogeneity. *Conservation Biology*. 21, 1475-1486.

Drechsler, M., Wätzold, F., Johst, K., Bergmann, H., Settele, J., 2007b. A model based approach for designing cost-effective compensation payments for conservation of endangered species in real landscapes. *Biological Conservation*. 140, 174-186.

Drechsler, M., Wätzold, F., Johst, K., Shogren, J.F., 2010. An agglomeration payment for cost-effective biodiversity conservation in spatially structured landscapes. *Resource and Energy Economics*. 32, 261-275.

Duffey, E., Morris, M.G., Sheil, J., Ward, L.K., Wells, D.A., Wells, T.C.E., 1974. Grassland ecology and wildlife management. Chapman and Hall, London.

Ellis, J.S, Knight, M.E, Darvill, B, Goulson, D., 2006. Extremely low effective population sizes, genetic structuring and reduced genetic diversity in a threatened bumblebee species, *Bombus sylvarum* (Hymenoptera: Apidae). *Molecular Ecology*. 15, 4375–4386.

Eppink, F.V., van den Bergh, J.C.J.H., 2007. Ecological theories and indicators in economic models of biodiversity loss and conservation: A critical review. *Ecological Economics*. 61, 284-293.

Eppink, F.V., van den Bergh, J.C.J.H., Rietveld, P., 2004. Modelling biodiversity and land use: urban growth, agriculture and nature in a wetland area. *Biological Economics*. 51, 201-216.

European Commission, 1999. Europe's Agenda 2000. Strengthening and widening the European Union. Draft of Commission information brochure for the general public on Agenda 2000. Final version 31.8. Priority Publications Programme 1999, X/D/5.

Falconer, K., 2000. Farm-level constraints on agri-environmental scheme participation: a transactional perspective. *Journal of Rural Studies*. 16, 379-394.

Faris, J.E., McPherson, W.W., 1957. Application of linear programming in an analysis of economic changes in farming. *The Review of Economics and Statistics*. 39, 421-434.

de Frahan, B.H., Buysse, J., Polomé, P., Fernagut, B., Harmignie, O., Lauwers, L., Van Huylenbroeck, G., Van Meensel, J., 2007. Positive Mathematical Programming for Agricultural and Environmental Analysis: Review and Practice. In: Handbook of Operations Research in Natural Resources. Eds: Weintraub, A., Romero, C., Bjørndal, T., Epstein, R.. Springer Science and Business Media. New York.

Food and Agriculture Organisation of the United Nations (FAO) Statistics available at: <http://faostat.fao.org/> Accessed 17th November 2010.

Fuller, R.M., 1987. The changing extent and conservation interest of lowland grasslands in England and Wales: A review of grassland surveys 1930 – 1984. *Biological Conservation*. 40, 281-300.

Fussell, M and Corbet, S.A., 1992. Flower usage by bumble-bees: a basis for forage plant management. *Journal of Applied Ecology*. 29: 451-465.

Goulson, D., 2003a. Bumblebees – behaviour and ecology, Oxford University Press, Oxford and New York.

Goulson, D., 2003b. Effects of introduced bees on native ecosystems. *Annual Review of Ecology and Systematics*. 34, 1-26.

Goulson, D., Darvill, B., 2004. Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? *Apidologie*. 35, 55-63.

- Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., 2006. Biotope associations and the decline of bumblebees (*Bombus* spp.). *Journal of Insect Conservation*. 10, 95-103.
- Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.E., Knight M.E., 2005. Causes of rarity in bumblebees. *Biological Conservation*. 122, 1-8.
- Goulson, D., Hughes, W.O.H., Derwent, L.C. and Stout, J.C., 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia*. 130, 267-273
- Goulson, D., Lye G.C., Darvill, B., 2008a. Decline and conservation of bumble bees. *Annual Review of Entomology*. 53, 191-208.
- Goulson, D., Lye, G.C. and Darvill, B., 2008b. Diet breadth, coexistence and rarity in bumblebees. *Biodiversity and Conservation*. 17, 3269-3288.
- Green, B.H., 1990. Agricultural intensification and the loss of habitat, species and amenity in British grasslands: a review of historical change and assessment of future prospects. *Grass and Forage Science*. 45, 365-372.
- Guzy, M.R., Smith, C.L., Bolte, J.P., Hulse, D.W., Gregory, S.V., 2008. Policy Research Using Agent-Based Modelling to Assess Future Impacts of Urban Expansion into Farmlands and Forests. *Ecology and Society*. 13, 37.
- von Hagen, E., 1994. Hummeln bestimmen. Ansiedeln, Vermehren, Schützen. Naturbuch-Verlag, Augsburg.

Hall Aitken, 2007. Outer Hebrides Migration Study. Final Report 2007. Report commissioned for Comhairle nan Eilean Siar, Western Isles Enterprise and Communities Scotland.

Hall, R.J., Hastings, A., 2007. Minimizing invader impacts: Striking the right balance between removal and restoration. *Journal of Theoretical Biology*. 249, 437-444.

Hance, W.A., 1952. Crofting in the Outer Hebrides. *Economic Geography*. 28, 37-50.

Hanley, N., Kirkpatrick, H., Oglethorpe., D., Simpson, I., MacDonald, A., 1996. Ecological-economic modelling of threatened heather moorland in the Northern Isles of Scotland. *Biodiversity and Conservation*. 5, 1207-1219.

Hanley, N., Kirkpatrick, H., Simpson, I., Oglethorpe., D., 1998. Principles for the Provision of Public Goods from Agriculture: Modeling Moorland Conservation in Scotland. *Land Economics*. 74, 102-113.

Hartig, F., Drechsler, M., 2009. Smart spatial incentives for market-based conservation. *Biological Conservation*. 142, 779-788.

Hastings, A., Hall., R.J., Taylor, C.M., 2006. A simple approach to optimal control of invasive species. *Theoretical Population Biology*. 70, 431-435.

Hayami, Y., & Ruttan, V.W., 1985. Agricultural development. An international perspective (revised edition). The Johns Hopkins Press. & Ruttan, Baltimore.

Hazell, P.B.R., Norton, R.D., 1986. *Mathematical Programming for Economic Analysis in Agriculture*. Macmillan Publishing Company, New York.

Heard, M.S., Carvell, C., Carreck, N.L., Rothery, P., Osborne, J.L., Bourke, A.F.G., 2007. Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. *Biology Letters*. 3, 638-641.

Heckbert, S., 2009. Experimental economics and agent-based models. 18th World IMACS/MODSIM Congress, Cairns, Australia. 13th-17th July 2009.

Heckbert, S., Adamowicz, W., Boxall, P., Hanneman, D., 2009. Cumulative effects and emergent properties of multiple-use natural resources. In: *Proceedings: MABS 2008*, Budapest, Hungary, May 10th-15th 2008.

Heckbert, S., Baynes, T., Reeson, A., 2010. Agent-based modelling in ecological economics. *Annals of the New York Academy of Sciences*. 1185, 39-53.

Heckelei, T., Britz, W., 2005. Models Based on Positive Mathematical Programming: State of the Art and Further Extensions. Plenary paper presented at the 89th EAAE Seminar, 3-5 February 2005, Parma. Paper available at:

www.ilr1.uni-bonn.de/agpo/publ/workpap/parma_heckelei_britz_proceedings%20_2_.pdf

Hengsdijk, H., Guanghuo, W., Van den Berg, M., Jiangdi, W., Wolf, J., Changhe, L., Roetter, R.P., Van Keulen, H., 2007. Poverty and biodiversity trade-offs in rural development: A case study for Pujiang county, China. *Agricultural Systems*. 94, 851-861.

Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, F.A., Niemelä, J., Rebane, M., Wascher, D., Watt, A. and Young, J., 2008. Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe – A review. *Agriculture, Ecosystems and Environment*. 124: 60-71

Highlands and Islands Enterprise, 2003. Western Isles Economic Update, October 2003. Network Economic Information.

Hodgson, J.G., Grime, J.P., Wilson, P.J., Thompson, K., Band, S.R., 2005. The impacts of agricultural change (1963-2003) on the grassland flora of Central England: processes and prospects. *Basic and Applied Ecology*. 6, 107-118.

Hopwood, J.L., 2008. The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation*. 141, 2632-2640.

House, A.P.N., MacLeod, N.D., Cullen, B., Whitbread, A.M., Brown, S.D., McIvor, J.G., 2008. Integrating production and natural resource management on mixed farms in eastern Australia: The cost of conservation in agricultural landscapes. *Agriculture, Ecosystems and Environment*. 127, 153-165.

Howitt, R.E., 1995. Positive Mathematical Programming. *American Journal of Agricultural Economics*. 77, 329 – 342.

Hunter, J., 1991. The claim of crofting. Mainstream. Edinburgh.

Husseneder, C., Brandl, R., Epplen, C., Epplen, J.T., Kaib, M., 1999. Within colony relatedness in a termite species: genetic roads to eusociality? *Behaviour*. 136, 1045-1063

Kaur, R., Srivastava, R., Betne, R., Mishra, K., Dutta, D., 2004. Integration of linear programming and a watershed-scale hydrologic model for proposing an optimized land-use plan and assessing its impact on soil conservation – A case study of the Nagwan watershed in the Hazaribagh district of Jharkhand, India. *International Journal of Geographical Information Science*. 18, 73-98.

Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Sanderson, R.A., Goulson, D., 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology*. 14, 1811-1820.

Kosior, A., Celary, W., Olejniczak, P., Fijal, J., Król, W., Solarz, W. and Plonka, P. (2007) The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: *Bombini*) of Western and Central Europe. *Oryx*. 41, 79-88.

Lloyd, R. J., Wibberley, G.P., 1977. Agricultural change. In: Davidson, J., Lloyd, R.J. (Eds), Conservation and agriculture. Wiley, London.

Love, J., 2003. Machair- Scotland's living landscapes. Scottish Natural Heritage, Battleby.

Lye, G.C., Park, K., Osborne, J., Holland, J., Goulson, D., 2009. Assessing the value of Rural Stewardship Schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biological Conservation*. 142, 2023-2032.

Macal, C.M., North, M.J., 2010. Tutorial on agent-based modelling and simulation. *Journal of Simulation*. 4, 151-162.

MacDonald, M., 2003. Bumblebees: Naturally Scottish. Scottish Natural Heritage. Battleby.

Mackenzie, A.F.D., 2007. The contribution of crofting in the 21st century. Committee of Inquiry on Crofting.

MacMillan, D.C., Marshall, K., Optimising capercaillie habitat in commercial forestry plantations. *Forest Ecology and Management*. 198, 351-365.

Mänd, M., Mänd, R., Williams, I.H., 2002. Bumblebees in the agricultural landscape of Estonia. *Agriculture, Ecosystems and Environment*. 89, 69-76.

McIntosh, A, Wightman, A., Morgan., D., 1994. Reclaiming the Scottish highlands: clearance, conflict and crofting. *Ecologist*. 2, 64-70.

Mathevet, R., Bouquet, F., Le Page, C., Antona, M., 2003. Agent-based simulations of interactions between duck population, farming decisions and leasing of hunting rights in the Camargue (Southern France). *Ecological Modelling*. 165, 107-126.

Messer, K.D., 2006. The conservation benefits of cost-effective land acquisition: A case study in Maryland. *Journal of Environmental Management*. 79, 305-315.

Mettepennington, E., Verspecht, A., Van Huylenbroeck, G., 2009. Measuring private transaction costs of European agri-environmental schemes. *Journal of Environmental Planning and Management*. 52, 649-667.

Meyer-Aurich, A., 2005. Economic and environmental analysis of sustainable farming practices – a Bavarian case study. *Agricultural Systems*. 86, 190-206.

Minh, T.T., Ranamukhaarachchi, S.L., Jayasuriya, H.P.W., 2007. Linear Programming-Based Optimization of the Productivity and Sustainability of Crop-Livestock-Compost Manure Integrated Farming Systems in Midlands of Vietnam. *Science Asia*. 33, 187-195.

Moisley, H.A., 1962. The Highlands and Islands. A crofting region? *Transactions and Papers (Institute of British Geographers)*. 31, 83-95.

Münier, B., Birr-Pedersen, Schou, J.S., 2004. Combined ecological and economic modelling in agricultural land use scenarios. *Ecological Modelling*. 174, 5-18.

Nalle, D.J., Montgomery, C.A., Arthur, J.L., Polasky, S., Schumaker, N.H., 2004. Modeling joint production of wildlife and timber. *Journal of Environmental Economics and Management*. 48, 997-1017.

Natural England, 2010. Information available to view at:

<http://www.naturalengland.org.uk/ourwork/farming/funding/closedchemes/esa/somersetlevsandmoors.aspx>.

Newbold, C., 1989. Semi-natural habitats or habitat recreation: conflict or partnership? In: *Biological Habitat Reconstruction*. Ed: Buckley, G.P. Belhaven, London.

Noordijk, J., Delille, K., Schaffers, A.P. and Sýkora, K.V., 2009. Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation*. 142, 2097-2103.

Pacini, C., Wossink, A., Giesen, G., Huirne, R., 2004a. Ecological-economic modelling to support multi-objective policy making: a farming systems approach implemented for Tuscany. *Agriculture, Ecosystems and Environment*. 102, 349-364.

Pacini, C., Giesen, G., Wossink, A., Omodei-Zorini, L., Huirne, R., 2004b. The EU's Agenda 2000 reform and the sustainability of organic farming in Tuscany: ecological-economic modelling at field and farm level. *Agricultural Systems*. 80, 171-197.

Pauwels, G., Gulinck, H., 2000. Changing minor rural road networks in relation to landscape sustainability and farming practices in West Europe. *Agriculture, Ecosystems and Environment*. 77, 95-99.

Perhans, K., Gustafsson, L., Jonsson, F., Nordin, U., Weibull, H., 2007. Bryophytes and lichens in different types of forest set-asides in boreal Sweden. *Forest Ecology and Management*. 242, 374-390.

Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P., Starfield, A., 2005. Conserving Species in a Working Landscape: Land Use with Biological and Economic Objectives. *Ecological Applications*. 15, 1387-1401.

Pollard, E., 1977. A method for assessing changes in abundance of butterflies. *Biological Conservation*. 12, 115-134.

Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R., Sherwood, A., 2004. Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation*. 121, 479- 494.

Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., Critchley, C.N.R., Sherwood, A., 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation*. 129, 192- 206.

Queller, D.C. and Strassmann, J.E., 2003. Eusociality. *Current Biology*. 13: 861-863.

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.

Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*. 39, 157-176.

Roux, E.A. and Korb, J., 2004. Evolution of eusociality and the soldier caste in termites: a validation of the intrinsic benefit hypothesis. *Journal of Evolutionary Biology*. 17, 869-875.

Rundlöf, M., Nilsson, H. and Smith, H.G., 2008. Interacting effects of farming practice and landscape context on bumble bees. *Biological Conservation*. 141, 417-426.

Saarinen, K., Valtonen, A., Jantunen, J., Saarnio, S., 2005. Butterflies and diurnal moths along road verges: Does road type affect diversity and abundance? *Biological Conservation*. 123, 403-412.

Saldarriaga Isaza, C.A., Gómez Bofill, W., Salgado Cabrera, H., 2007. Cost-effective species conservation: an application to Huemul (*Hippocamelus bisulcus*) in Chile. *Environment and Development Economics*. 12, 535-551.

Schlüter, M., Pahl-Wostl, C., 2007. Mechanisms of Resilience in Common-pool Resource Management Systems: an Agent-based Model of Water Use in a River Basin. *Ecology and Society*. 12, 4.

Schmid, E., Sinabell, F., 2005. Using the Positive Mathematical Programming Method to Calibrate Linear Programming Models. Discussion Paper DP-10-2005. Institute for Sustainable Economic Development.

Schmid-Hempel, P. 1998. Parasites in social insects. – Princeton University Press.

Schreinemachers, P., Berger, T., Aune, J.B., 2007. Simulating soil fertility and poverty dynamics in Uganda: A bio-economic multi-agent systems approach. *Ecological Economics*. 64, 387-401.

Stewart, A., 1994. The conservation importance of machair systems of the Scottish Islands, with particular reference to the Outer Hebrides. In: *The islands of Scotland: Living marine heritage*. Ed: Baker, J.M., Usher, M.B. HMSO.

Stewart, K., 2005. Crofts and crofting: past, present and future. Mercat press Ltd., Edinburgh.

Stewart, G.B., Pullin, A.S., 2008. The relative importance of grazing stock type and grazing intensity for conservation of mesotrophic 'old meadow' pasture. *Journal of Nature Conservation*. 16, 175-185.

Stoate, C., Boatman, N.D., Borralho, R.J., Rio Carvalho, C., de Snoo, G.R. and Eden, P., 2001. Ecological Impacts of arable intensification in Europe. *Journal of Environmental Management*. 63, 337-365.

Strijker, D., 2005. Marginal lands in Europe – causes of decline. *Basic and Applied Ecology*. 6, 99-106.

Stroud, D.A., 1998. Crofting and bird conservation on Coll and Tiree. *International Wader Studies*. 10, 1-68.

Sutherland, R. and Bevan, K., 2001. Crofting in the 21st Century. A study for SEERAD. Report on Survey of Crofting Incomes and Responses to Agricultural Policy Changes. SAC.

Svensson, B., Lagerlöf, J., Svensson, B.G., 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems and Environment*. 77, 247-255.

The R Foundation for Statistical Computing, 2010. R version 2.11.1. (2010-05-31).

Thompson, D.B.A., MacDonald, A.J., Marsden, J.H., Galbraith, C.A., 1995. Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation*. 71, 163-178.

Tucker, J.L., Rideout, D.B., Shaw, R.B., 1998. Using linear programming to optimize rehabilitation and restoration of injured land: an application to US army training sites. *Journal of Environmental Management*. 52, 173-182.

Tyynelä, T., Otsamo, R., Otsamo, A., 2003. Indigenous livelihood systems in industrial tree-plantation areas in West Kalimantan, Indonesia: Economics and plant-species richness. *Agroforestry Systems*. 57, 97-100.

Vanslebrouck, I., Van Huylenbroeck, G., Verbeke, W., 2002. Determinants of the willingness of Belgian farmers to participate in agri-environmental measures. *Journal of Agricultural Economics*. 53, 489-511.

Wätzold, F., Drechsler, M., Armstrong, C., Baumgärtner, S., Grimm, V., Huth, A., Perrings, C., Possingham, H., Shogren, J.F., Skonhøft, A., Verboom-Vasiljev, J., Wissel, C., 2006. Ecological-economic Modeling for Biodiversity Management: Potential, Pitfalls, and Prospects. *Conservation Biology*. 20, 1034-1041.

Weibull, A., Östman, Ö., Granqvist, A., 2003. Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity and Conservation*. 12, 1335-1355.

Wells, T.C.E., Sheail, J., 1988. The effects of agricultural change on the wildlife interest of lowland grasslands. In Park, J.R. (Ed) Environmental management in agriculture: European perspectives (pp186-201). Belhaven Press, London.

Westphal, C., Steffan-Dewenter, I., Tscharntke, T., 2006. Foraging trip duration of bumblebees in relation to landscape-wide resource availability. *Ecological Entomology*. 31, 389-394.

Williams, P.H., 1982. The distribution and decline of British Bumble Bees (*Bombus Latr.*). *Journal of Apicultural Research*. 21, 236-245.

Williams, P.H., 1986. Environmental change and the distribution of British bumble bees (*Bombus Latr.*). *Bee World*. 67, 50-61.

Williams, P.H., 1988. Habitat use by bumble bees (*Bombus spp.*). *Ecological Entomology*. 13, 223-237.

Williams, P.H. and Osborne, J.L., 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie*. 40, 367-387.

Willis, D., 1991. The story of crofting in Scotland. John Donald Publishers Ltd., Edinburgh.

Willis, D., 2001. Crofting. John Donald Publishers Ltd., Edinburgh.

Zuur, A.F., Ieno, E.N., Walker, N.J., Savaliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science and Business Media, New York.