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The use of off-farm habitats by foraging bumblebees in agricultural landscapes: implications for conservation management

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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. We conducted a comparative study to assess bumblebees and flower abundance on farmed and off-farm habitats in two low-intensity systems in the UK, the Somerset Levels and the Outer Hebrides. In both farming systems, both on- and off-farm habitats contributed to the mosaic of bumblebee forage. In the Somerset Levels, track edges and road verges were particularly important sources of forage for long-tongued bumblebees. Cattle-grazed pasture in Somerset and winter-grazed pasture in the Outer Hebrides were also notable sources of bumblebee forage. Non-agricultural habitats need to be integrated into local land management plans to ensure the provision of forage for bumblebees throughout the breeding season.

Bombus / foraging / habitat use / road verge / grazing

1. INTRODUCTION

Agricultural intensification 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 (Robinson and Sutherland 2002; Goulson et al. 2005, 2006). Of the 25 bumblebee species native to Britain, three are now extinct and six others are formally listed as being threatened (Benton 2006; Goulson et al. 2008a, b). 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 2003; Williams and Osborne 2009). However, vast areas of these semi-natural habitats have been lost over the past century following changes to agricultural practices (Pywell et al. 2005; Carvell et al. 2006; Chamberlain et al. 2000; Stoate et al. 2001). Consequently, 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 within the UK are the crofting systems found in northwest Scotland and the Somerset Levels in southwest England.

Agriculture in crofting areas traditionally operates on a small scale, with few artificial inputs. Traditional crofting practices include areas of

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lowland grassland grazed during the winter months and livestock relocated to moorland grazing during the summer. Consequently, crofted areas can 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 *Bombus distinguendus* and *Bombus 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 *Bombus sylvarum* and *Bombus ruderarius* (Benton 2006). 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.

Traditionally both these agricultural systems provide essential grassland foraging habitats for bumblebees and internationally important habitats for many other taxa (Love 2003; Natural England 2010). 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 densities were recorded foraging on these off-farm habitats compared to farmed habitats (Mänd et al. 2002). Redpath et al. (2010) 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 paper, we conduct a comparative study to assess the value of farmed and off-farm habitats in providing forage for bumblebees in two low-intensity agricultural systems in the UK: a crofting

system threatened by intensification in the Outer Hebrides and a low-intensity system in the Somerset Levels.

2. METHODS

2.1. Study sites

We conducted our study in the Outer Hebrides and the Somerset Levels in two consecutive years to enable us 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, we concentrated our 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"). We 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 1.

2.2. Bumblebee sampling techniques

Bumblebee surveys were carried out on each habitat between the 27th July and 15th August 2009 in the Outer Hebrides. Six replicate sections of each habitat (except summer-grazed pasture) were identified and separated from one another by a minimum distance of 100 m. This distance was constrained by the small sizes of the two study areas; it should be noted that bumblebees will forage over much larger distances than this, so that the same individuals may have visited more than one replicate section. In most instances, agricultural sections were equivalent to a field. Due to access restrictions, we were only able to survey five sections of summer-grazed pasture in the

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

Habitat	Definition	Transect area surveyed (m ²)	
		Outer Hebrides	Somerset Levels
Silage	Outer Hebrides: cultivated land sown with a grass crop or mixed cereals (barley, oats and rye) Somerset Levels: land left to regenerate to form a natural grass crop/grazed for a short period after cutting	400–600	1,372–2,568
Fallow	Cultivated land, not seeded for ≥ 1 years	1,200–3,700	0
Pasture	Outer Hebrides: land grazed throughout the year by sheep, cattle or both	1,000–3,200	172–2,900
Cattle-grazed pasture	Somerset Levels: land grazed by cattle throughout the year		
Winter pasture	Outer Hebrides: land grazed between September and May	800–6,000	0
Track edges	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	500–1,300	700–1,300
Road verges	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	700–1,700	840–1,100

Outer Hebrides. In this area, 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, and each individual section was surveyed once for foraging bumblebees in August 2009. In 2010, we extended our 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. The length of transects varied in accordance to the area of each habitat (shown in Table I). In fields (typically sections of pasture or silage), transects were conducted along a zigzag route to ensure that a representative area of the habitat was surveyed. All foraging bumblebees observed within 2 m on either side of the transects

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, but only 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 transects were recorded, in addition to the forage plant species being utilised. This survey methodology is taken from Redpath et al. (2010) who 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 transects were walked. Bumblebees observed foraging within 2 m of the selected side of the transects were recorded as previously described.

All surveys took place in dry weather and when the temperature was above 12°C in accordance with the protocols outlined by Carvell (2002). The number and species of any livestock present along a transect were also recorded.

2.3. 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 0.5×0.5-m quadrat. A total of 200 quadrats were recorded in each 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 transects 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 in 2009 in the Outer Hebrides and once each month between June and August 2010 on the Somerset Levels to correspond with the monthly bee walks. The inflorescences of all flowers utilised by foraging bumblebees were recorded, as in Redpath et al. (2010).

2.4. Data analysis

2.4.1. 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 for Statistical Computing 2010). The abundance of long- and short-tongued foraging bumblebees was examined in separate analyses. 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, 2008a; Pywell et al. 2005). For statistical analysis, we grouped together long-tongued species (*B. distinguendus*, *B. muscorum*, *Bombus pascuorum* and *Bombus hortorum*) and short-tongued species (*Bombus lapidarius*, *Bombus lucorum*, *Bombus terrestris*, *Bombus jonellus*, *Bombus pratorum*, *Bombus barbutellus* and *Bombus sylvestris*). As very few males were recorded in either study area, species were only subdivided by tongue length for analysis. The Outer Hebrides and Somerset Levels datasets were analysed separately. All models used quasi-Poisson errors except the July short-tongued bumblebee dataset where the data were not over-dispersed and Poisson errors were more appropriate. 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.

2.4.2. Forage plant datasets

The availability of forage was examined using generalised linear models as described above. One model using quasi-Poisson errors was constructed for the Outer Hebridean dataset, and Gaussian errors were utilised in models for the Somerset Levels. 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 that we observed bumblebees foraging upon.

The relationship between bumblebee abundance and forage availability was examined using a gener-

alised linear model for each month of the survey, using quasi-Poisson errors and area as an offset except for the July short-tongued bumblebees in which Poisson errors were utilised.

3. RESULTS

3.1. Habitat and bumblebee abundance

3.1.1. Outer Hebrides

A total of 494 foraging bumblebees belonging to five species were recorded across all habitat types in 2009 (Table II). All species known to be found within the Outer Hebrides study area were recorded foraging in at least one of the habitats surveyed.

The abundance of long-tongued bumblebees varied significantly between habitat types ($\chi^2_5=12.35$, $P=0.03$; Table III; Figure 1a). Following model simplification where temperature and wind speed were removed, only habitat remained in the final model, explaining 81% of variation. Significantly fewer long-

tongued bumblebees were observed on pasture than winter-grazed pasture (Table III). Comparing the median number of bumblebees recorded on each habitat highlights that nine times more bumblebees were supported by pasture which was only grazed in the winter, rather than pasture subject to year-round grazing. The abundance of short-tongued bumblebees also varied with habitat type (Figure 1b), but the relationship was not significant ($\chi^2=5.25_5$, $P=0.386$).

3.1.2. 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 II). 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 ($\chi^2_2=0.02$, $P=0.992$, Table IIa). Wind speed correlated

Table II. The percentage of each bumblebee species observed foraging on all habitats in the Outer Hebrides in 2009 (total $n=494$) and throughout the field season on the Somerset Levels in 2010 (total $n=439$).

Species	% Total bumblebees			
	Outer Hebrides	Somerset Levels		
		June	July	August
<i>B. lapidarius</i>	0	27	53	43
<i>B. lucorum/terrestris</i> ^{a,b}	29	33	26	8
<i>B. muscorum</i>	61	0	0	0
<i>B. pascuorum</i>	0	26	14	49
<i>B. distinguendus</i>	7	0	0	0
<i>B. pratorum</i>	0	11	0	0
<i>B. sylvestris</i>	0	3	<1	0
<i>B. hortorum</i>	3	0	5	0
<i>B. jonellus</i>	<1	0	<1	0
<i>B. barbutellus</i>	0	0	<1	0
Unidentified	0	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

^b Only *B. lucorum* is present in the Outer Hebrides study area

Table III. The association between habitat on long-tongued bumblebee abundance in the Outer Hebrides.

	Arable		Fallow		Pasture		Road verges		Track edges	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<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

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 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

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 m/s.

Habitat was a significant predictor of long-tongued bumblebee abundance in July ($\chi^2_3=42.95$, $P<0.0001$; Figure 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 the median number of bumblebees recorded on each habitat illustrating that nine times more bumblebees were observed on off-farm habitats (Table IV; Figure 2b). 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 on surveys where the temperature was recorded as 25°C or above, with all observations made when the temperature ranged from 21.6°C to 24.9°C.

The association between habitat and short-tongued bumblebee abundance in July contrasted to 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 ($\chi^2_3=22.65$, $P=<0.0001$; Figure 3b; Table IV), but only 35% of the observed variation was

explained by this model. Higher wind speeds and temperatures were associated with lower numbers 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. Track edges supported the greatest densities of long-tongued bumblebees, with 39% more than on silage or cattle-grazed pasture ($\chi^2_3=10.96$, $P=0.012$; Figure 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 (Figure 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 ($\chi^2_1=3.84$, $P=0.050$).

3.2. Habitat and the availability of bumblebee forage plants

The abundance of bee-flower inflorescences varied between habitats in the Outer Hebrides, with forage availability greatest on road verges, unmanaged track edges and

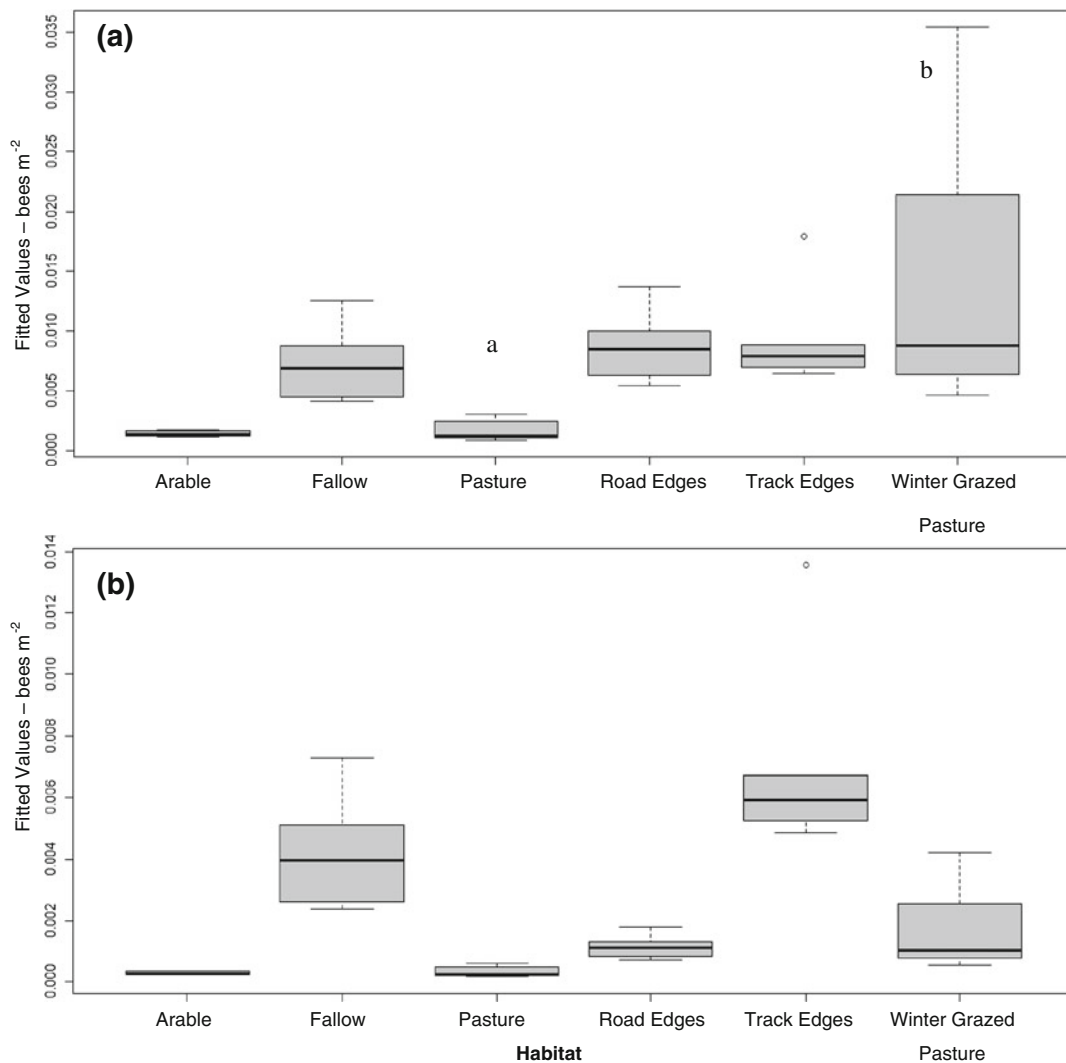


Figure 1. a, b Box plots showing fitted values from the model for long-tongued bumblebee abundance (a) and the model for short-tongued bumblebee abundance (b) across six different habitats in the Outer Hebrides. Boxes represent the location of the middle 50% of the data, and the whiskers indicate the interquartile range of the data. a and b denote significant differences between habitats.

winter-grazed pasture ($\chi^2=23.2$, $P=0.0003$; Table V). Arable and summer-grazed pasture had the lowest densities of bumblebee forage with fewer than 10% of total bee-flower 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 V), yet supported equal numbers of foraging long-tongued bumblebees. Although fallow contained few bee-flowers, it

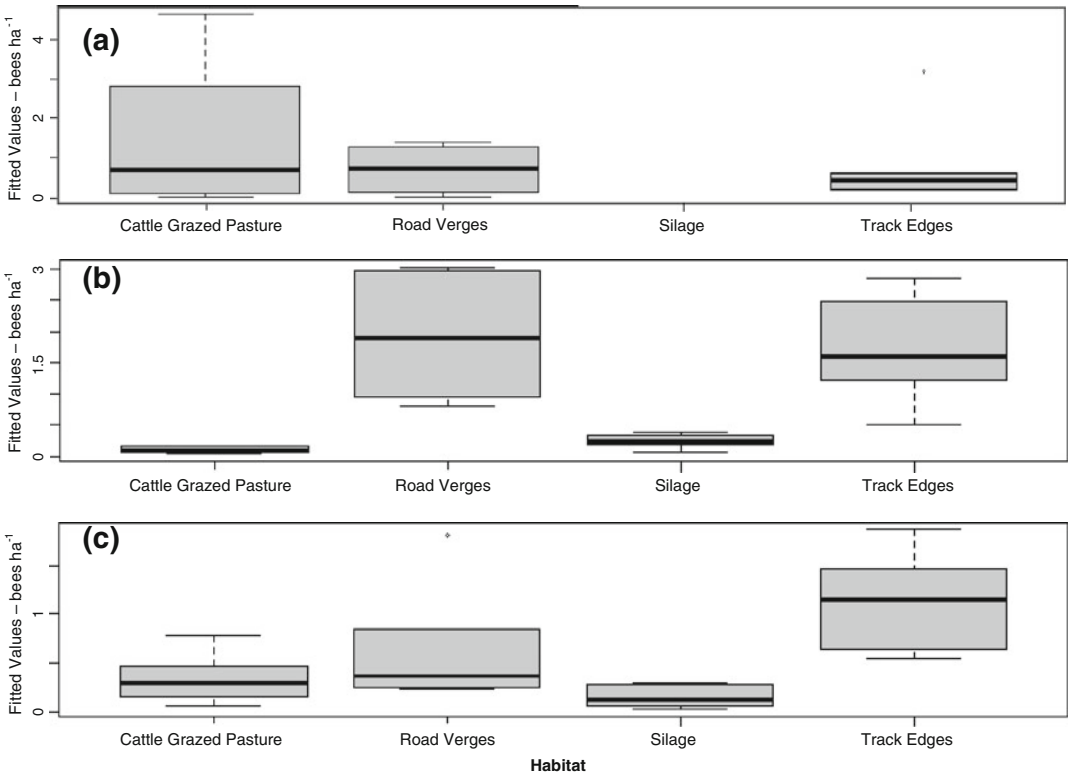


Figure 2. a–c Box plots showing fitted values from the models for long-tongued bumblebee abundance across four different habitats in the Somerset Levels. **a** The data for June, **b** July and **c** August 2010. Boxes represent the location of the middle 50% of the data, and the whiskers indicate the interquartile range of the data.

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 ($\chi^2_2=3.80$, $P=0.150$; Figure 4a). In July, road verges supported significantly fewer bee-flowers than either silage or cattle-grazed pasture ($t=2.19$, $P=0.041$, $t=-2.83$, $P=0.011$ respectively; Figure 4b), with <50% of inflorescences present in either farmed habitat. No other significant differences were identified between habitats in July. Habitat was not a significant predictor of forage plant availability in August ($\chi^2_3=4.99$, $P=0.173$).

3.3. The relationship between bumblebee abundance and forage availability

Bee-flower inflorescence density was a significant predictor of long-tongued bumblebee abundance in the Outer Hebrides ($\chi^2_1=4.75$, $P=0.029$), explaining 64% of the variation observed. The variation in abundance of bee-flower inflorescences broadly reflects the distribution of long-tongued bumblebees in the Outer Hebrides. However, the model explains considerably less variation than the model that used habitat as the explanatory variable, suggesting that habitat is a better predictor of long-tongued bumblebee abundance. Forage availability was not a significant predictor of

Table IV. The association between habitat and long-tongued and short-tongued bumblebee abundance on the Somerset Levels in July and August 2010.

	July						August												
	Cattle grazed			Road verge			Track edge			Cattle grazed			Road verge			Track edge			
	<i>t</i>	<i>p</i>	<i>z</i>	<i>t</i>	<i>p</i>	<i>z</i>	<i>t</i>	<i>p</i>	<i>z</i>	<i>t</i>	<i>p</i>	<i>z</i>	<i>t</i>	<i>p</i>	<i>z</i>	<i>t</i>	<i>p</i>	<i>z</i>	
Long-tongued	Road verge	2.63	0.016																
	Track edge	2.84	0.011		0.623	0.541							1.06	0.304					
	Silage	0.311	0.759	-3.81	0.001	0.001	-3.97	0.001	0.001				1.63	0.120	0.89	0.386			
Short-tongued	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	0.0001	4.15	<0.0001	4.15	<0.0001	<0.0001	4.15	<0.0001	4.15	<0.0001	4.15	<0.0001	4.15	<0.0001

The *t*, *z* and *p* values are derived from pair-wise comparisons made between each of habitat. Negative *t* or *z* values show that the habitat listed along the rows of the table supported 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

short-tongued bumblebee abundance ($\chi^2_1 = 0.41, P = 0.524$).

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 ($\chi^2_1 = 1.01, P = 0.906$), which may be due to a reduction in the number of inflorescences suitable for long-tongued species. 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 type was a better predictor of both long- and short-tongued bumblebee abundances than numbers of flowers.

3.4. Bumblebee forage plant choices

A total of ten flowering plant species were utilised by foraging bumblebees throughout the study in the Outer Hebrides (Table VI). 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 to the Outer Hebrides, few visits were made to the Asteraceae by foraging bumblebees on the Somerset Levels (Table VI). *Trifolium repens* was particularly important to

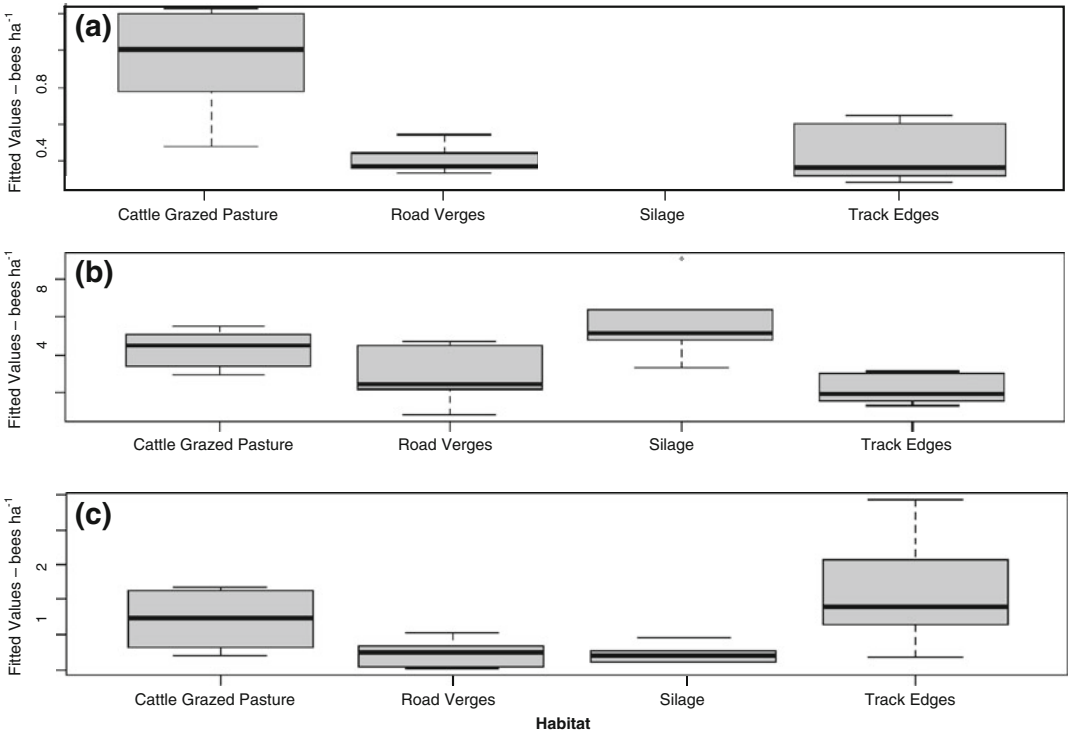


Figure 3. a–c Box plots showing fitted values from the models for short-tongued bumblebee abundance across four different habitats in the Somerset Levels. **a** The data for June, **b** July and **c** August 2010. Boxes represent the location of the middle 50% of the data, and the whiskers indicate the interquartile range of the data.

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. The abundance of this plant species was also a significant

predictor of *B. lapidarius* abundance in July ($\chi^2_1=10.40$, $P=0.001$). Cattle-grazed pasture and silage fields supported the greatest abundances of *T. repens* throughout the survey period. Although members of the Fabaceae

Table V. The association between habitat and forage plant abundance in the Outer Hebrides.

	Arable		Fallow		Pasture		Road verges		Track edges	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<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

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

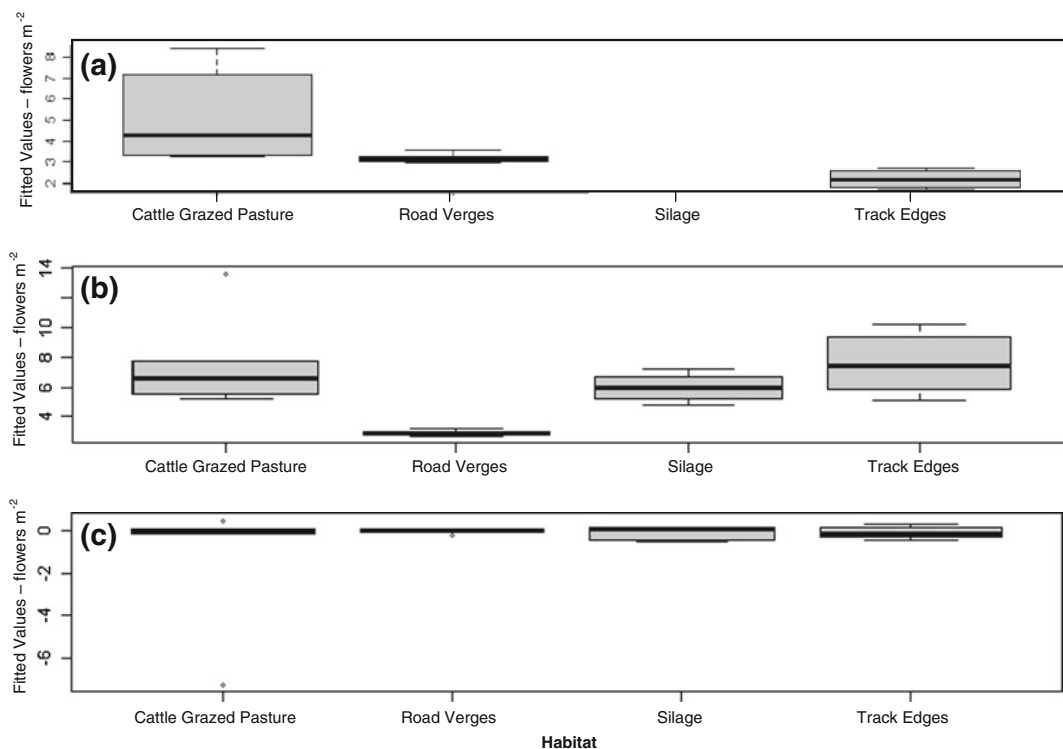


Figure 4. a–c Box plots showing fitted values from the models for the abundance of bumblebee forage plants on four different habitats in the Somerset Levels. **a** The data for June, **b** July and **c** August 2010. Boxes represent the location of the middle 50% of the data, and the whiskers indicate the interquartile range of the data.

were also important for long-tongued bumblebees in June, this group of bumblebees was predominantly recorded foraging on *Rubus fruticosus* and *Epilobium* spp. in July and August. These plants were both confined to road verges and track edges

4. DISCUSSION

4.1. 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).

We 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) 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.

However, these non-agricultural habitats 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)

Table VI. The flower species visited by foraging bumblebees in the Outer Hebrides and the Somerset Levels.

Flower species	Family	Outer Hebrides		Somerset Levels					
				June		July		August	
		Long (%)	Short (%)	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</i> spp.	Onagraceae	–	–	0	0	21	17	28	42
<i>Hypericum</i> spp.	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

The number of visits made by long and short-tongued bumblebees to each species is shown as percentages

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.

On the Somerset Levels, cattle-grazed fields and silage provided an abundance of key forage plants for short-tongued bumblebee species compared to the other available habitats. Where silage is cut early in the

season, this management practice creates 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. In our study, 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.

4.2. Bumblebee floral resource use

In accordance with previous studies (e.g. Goulson and Darvill 2004; Redpath et al. 2010), our data show that bumblebees utilise a few key forage plant species rather than particularly diverse floral assemblages. Of the ten 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 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 were short-tongued species. Bumblebees in this group 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.

4.3. Implications for conservation management

Both this study and that by Redpath et al. (2010) 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. Our 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 bumblebee forage for a lengthy period during the early–mid flight period due to the prevalence of *T. repens* in these habitats.

The rural road network may provide important habitats for farmland biodiversity (Pauwels and Gulinck 2000), and the results of our study suggest that road verges and track edges are of greater value to long-tongued bumblebees than farmed habitats, particularly in intensively managed agricultural landscapes. With the decline of pollinators and the potential negative impacts on the ecosystems services that they provide, the use of these off-farm habitats for supporting flower-visiting insects may be increasingly important. Indeed, road verges have the potential to be managed for the benefit of a range of other insects in addition to bees, including Lepidoptera and Coleoptera (e.g. Landis et al. 2000; Saarinen et al. 2005; Noordijk et al. 2009; Decourtye et al. 2010).

The value of track edges and road verges to long-tongued bumblebees and other pollinators 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. As road verges are found on non-agricultural land, they fall outside the scope of agri-environment scheme payments to encourage beneficial management practices. We therefore suggest that road verges be 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.

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Utilisation, par les bourdons, des habitats non-cultivés dans les paysages agricoles: implications dans des aménagements à but de conservation.

***Bombus* / approvisionnement / utilisation des habitats / bord de route / pâturage**

Die Nützlichkeit von Habitaten außerhalb der landwirtschaftlichen Flächen in Agrargebieten für sammelnde Hummeln: Bedeutung für den Artenschutz

***Bombus* / Sammeln / Habitatnutzung / Straßenrand / Weide**

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