WHAT FORAGING RESOURCES ARE USED BY BUMBLEBEES ON THE SOMERSET LEVELS AND WHICH ARE KEY TO RETAINING BUMBLEBEE DIVERSITY?

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Abstract

The Somerset Levels supports a number of scarce bumblebee species, whose national decline has been linked to the loss of available forage resources – nectar and pollen from flowering plants. The study reported here examines which plant species are used by bumblebees on the Somerset Levels, and the extent to which different bumblebee species foraged from different sources. The study was undertaken from May to July 2010 as part of an undergraduate dissertation (Iles, 2010), which forms the basis of this paper. Bumblebee foraging activity was recorded along fixed transects at three sites: Shapwick Heath, Ham Wall and Westhay NNRs. The study found eleven bumblebee species to be present, and showed that the forage resources available were partitioned between them, with different plants favoured by different bumblebee species. The scarce bumblebees on the study sites foraged disproportionately from certain species of the pea family (Fabaceae).

INTRODUCTION

Considerable changes have occurred in British agriculture since 1945, resulting in an increasingly industrialised and homogeneous farmed landscape. Associated with these changes have been declines in many animals and plants specialising in semi-natural habitats and less-intensive farmed landscapes, whilst habitat 'generalists' have not declined to the same extent, if at all (Robinson and Sutherland 2002).

This pattern of some species declining while others remain unaffected can be seen amongst populations of British bumblebees (genus *Bombus*), where many species are in decline but six remain abundant (Goulson *et al.* 2005). Bumblebees are of especial significance as keystone species providing pollination for many plant species that might be expected to decline in the wake of bumblebee declines; and there is clearly an economic argument for conserving bumblebees based on the commercial services they provide as pollinators for cash crops (Benton 2006).

Agricultural changes impacting on bumblebees are summarised by Williams and Osborne (2009) and include:

- Industrialisation of arable farming, particularly drainage and expansion of field size resulting in loss of field margins and hedgerows.
- 'Improvement' of pasture through drainage, use of fertilisers and the sowing of grass monocultures.
- An end to rotational farming and the use of clover leys.
- A change from hay production to silage.
- The widespread use of pesticides, including herbicides and insecticides.

As a result of the above changes, forage sources used by bumblebees – wild flowers from which the bumblebees obtain pollen and nectar – have declined in terms of both range and abundance (Carvell *et al.*

2006), and the scale of their decline appears to have been greater than that of plant species generally. Especially worrying has been the widespread loss of Fabaceae (vetches, peas, clovers, etc), and in particular Red Clover (*Trifolium pratense*), which is often cited as a key forage source for bumblebees (Bumblebee Working Group 2002; Goulson and Darvill 2004) and is a significant component of less intensive agricultural systems.

The so-called 'big six' bumblebee species – *Bombus terrestris* (Buff-tailed Bumblebee), *B. lucorum* (White-tailed Bumblebee), *B. pascuorum* (Common Carder-bee), *B. pratorum* (Early Bumblebee), *B. lapidarius* (Red-tailed Bumblebee) and *B. hortorum* (Garden Bumblebee) – remain common and widespread. A further six species of 'cuckoo' bumblebees in the sub-genus *Psithyrus*, all social parasites which take over nests of 'true' bumblebee species, also appear to have been largely unaffected by agricultural changes. However, most other species of bumblebee resident in Britain are in decline and have become increasingly restricted to areas with high concentrations of semi-natural habitat. These habitats are varied, including brownfield mosaics along the Thames estuary, the shingle at Dungeness, chalk grassland on Salisbury Plain, and machair and moorland in the Outer Hebrides; what links these habitats, however, is that they are all flower-rich (Benton 2006).

Another habitat that has retained scarce bumblebees is the wetland of the Somerset Levels, which has one of only seven extant populations of *B. sylvarum* (Shrill Carder-bee) in Britain and one of the few southern populations of *B. muscorum* (Moss Carder-bee), a specialist of damp habitats whose strongest populations exist in Scotland (Williams 2009; Benton 2006). The Levels are unusual amongst habitats supporting rare bumblebees in that, although floristically rich and having escaped much agricultural improvement (Whitefield 2009), they do not support obvious, large concentrations of plants suitable for foraging bumblebees (P. Rayner, pers. comm.). The study reported in this paper investigates what plants bumblebees are using for forage on the Somerset Levels, and in particular which of these are being used by the scarcer species. This may be important, as one popular (if contested) explanation of why some bumblebee species have remained common whilst others have declined is that declining species forage from a restricted range of plant species for nectar and pollen, whereas common species have a broader, more generalised diet (Goulson and Darvill 2004).

The Somerset Levels present a conundrum: scarce bumblebee species persist in the area, yet many of the plant species on which they forage elsewhere are absent, and the area lacks obvious, large, flower-rich sources of forage on which they might feed (P. Rayner pers. comm.; pers. obs.). The area has not been extensively improved for agriculture, and consists of a mosaic of cattle pasture, hay meadows and reed-bed. Some White Clover (*Trifolium repens*) is present in pastures, but it is unclear how populations of Fabaceae-dependent bumblebees might survive here. The pastures are dissected by drainage ditches and drove tracks as well as hedgerows, and it has been suggested that these linear habitats might provide important forage sources for the scarcer bumblebees; Comfrey (*Symphytum officinale*), for example, is available through much of the year on ditch banks and verges while, late in the year, Red Bartsia (*Odontites verna*) may be conspicuous along the droves (P. Rayner pers. comm.; Benton 2006).

BUMBLEBEE LIFE CYCLES AND FORAGING – BACKGROUND

Bumblebees are social organisms forming annual colonies, founded by a queen bumblebee that relies on a caste of infertile workers foraging for pollen and nectar with which to raise male and female reproductives (Heinrich 1979; Goulson 2010). Queen bumblebees emerge from hibernation in the spring; the exact time of emergence varies between species and with latitude, with emergence earlier in warmer southern areas. The queens need to feed following hibernation, to establish a nest, lay eggs and to provide nectar and pollen for the growing larvae (Benton 2006). Availability of forage at this stage of the bumblebee lifecycle is an important factor in determining the success or failure of the nest (Goulson 2010). The common 'big six' bumblebees emerge by the end of March, the cuckoo-bees (subgenus *Psithyrus*) emerge during April, while some grassland bumblebees such as *B. sylvarum* and *B. humilis* (Brown-banded Carder-bee) emerge during late May (Benton 2006; Edwards and Jenner 2004). The time of emergence is probably related to the flowering of suitable forage sources – few forage sources are available in hay meadows, marshy areas and calcareous grassland before mid-May, yet woodland edges and hedgerows will often support plants that provide suitable forage earlier (Benton 2006).

The larvae develop into infertile worker bees that will take over foraging duties from the queen, who continues to lay eggs which develop into further generations of worker bees and, as the colony develops, into males and fresh queens. For this to occur, a sufficient supply of nectar and pollen must be available within foraging distance of the nest. If a bumblebee nest is to rear potential future founders of colonies it must have ready access to a continuous supply of forage from a queen's first emergence from hibernation until males and young queens leave the nest, and this will require the use of different forage sources over time (Heinrich 1979).

Certain plant species are heavily used by bumblebees for foraging; many others are used scarcely or not at all. Heinrich (1979) explored the preferences of foraging bumblebees in terms of energy efficiency. Different plant species have differing morphologies, which require the bee to perform differing physical acts to obtain the pollen or nectar reward, something learned by individual bees. This encourages specialisation by individual bees on particular plant species, within a wider pattern of bumblebee species displaying a preference for certain plant species based on differing flower and bumblebee morphologies – of which the tongue length of bumblebees is the most significant. Individual bees within a colony may differ in terms of their preferred forage source, meaning that the colony is able to exploit a wide range of flower species available (Heinrich 1979; Goulson 2010). One cause of specialisation is that workers within a nest vary in size; this has implications for their forage specialism, as, for example, small bees can access flowers inaccessible to larger bees.

Bumblebees have a high metabolic rate (Goulson 2010) and, as workers need to not only return a supply of pollen and nectar to the nest to feed the larvae but also forage for themselves and cover the energy cost of their flight, there is considerable pressure to forage as efficiently as possible. This efficiency can be measured in terms of both the energy required to forage and the time taken, as slower foraging reduces the rate at which a colony receives energy (Heinrich 1979). Availability of suitable forage sources within easy reach of the nest will therefore help to determine the productivity of the colony.

As already noted, a key morphological distinction amongst bumblebees is tongue length, which impacts on the efficiency with which they can forage from flowers with different corolla lengths; bumblebees with short tongues cannot readily access nectar from flowers with deep corollae, such as Foxglove (*Digitalis purpurea*) or Red Clover (*Trifolium pratense*), whilst the long tongues of other bumblebees may be inefficient mechanisms for foraging from flowers with more easily accessible nectar, such as Bramble (*Rubus fruticosus* agg.) (Heinrich 1979; Goulson 2010). Amongst British bumblebee species, tongue length varies from *c*. 8mm to *c*. 14mm. Of the species present on the study sites, *B. hortorum* has by some way the longest tongue. The four species from the sub-genus *Thoracobombus* (the widespread *B. pascuorum* and the scarce *B. humilis, B. muscorum* and *B. sylvarum*) are also considered long-tongued; the others are short-tongued (Goulson *et al*. 2005). Declines have been most prevalent amongst long-tongued bumblebees.

Less work has been carried out on pollen-gathering and the efficiency with which this is carried out, although in comparison with nectar-gathering it is evident that pollen is sourced from a more restricted range of flower species. Whilst pollen is invariably gathered from nectar sources, some are preferred to others – plants in the family Fabaceae are preferred, whereas Asteraceae (daisy family) and Boraginaceae (borage family) are frequently visited for nectar but rarely for pollen (Goulson *et al*. 2005). The narrower range of species used suggests that shortages of suitable pollen sources may limit bumblebee populations more than shortages of nectar sources (Goulson 2010).

Individual species vary in the degree of foraging specialisation shown. Goulson *et al*. (2005) observed that the species that have declined are often those showing a strong association with Fabaceae, like the rare *B. humilis* which was observed making 92.6% of its pollen-foraging trips to Fabaceae. This species also had the narrowest range of nectar sources, with Red Clover and Common Bird's-foot-trefoil (*Lotus corniculatus*) being the main plant species involved. The diet of the common and widespread species such as *B. lapidarius* and *B. lucorum/terrestris* was noted as being much wider, although an exception was the widespread but long-tongued *B. hortorum*, which had a strong association with Red Clover on Salisbury Plain (82% of pollen-foraging visits; Goulson and Darvill 2004). Carvell *et al*. (2006) distinguished the long-tongued from the short-tongued bees, associating the former with Fabaceae and Black Horehound (*Ballota nigra*), and the latter with Asteraceae. There is evidence that even the longer-tongued, rarer bumblebees may be quite flexible in their forage requirements; for example,

Viper's Bugloss (*Echium vulgare*) is commonly used as forage by *B. sylvarum*, yet may be absent from many of the habitats in which this bee occurs (Bumblebee Working Group 2002).

METHODS

Study sites

Three wetland sites were studied: the National Nature Reserves (NNRs) at Shapwick Heath, Ham Wall and Westhay. The sites were chosen for their size, their convenience of access, the fact that they were all under conservation management, and because they were known to support a range of bumblebee species including the rare *B. sylvarum* and *B. muscorum* (Saunders 2008). Although all are wetland sites containing extensive reed-beds, they have different histories and contain different potential habitats for bumblebees.

At Shapwick Heath NNR the study area included wet meadows around Canada Farm, as well as sections of road verge. The Shapwick meadows contained a variety of suitable forage plants for bumblebees – Fabaceae such as Common Bird's-foot-trefoil, White Clover and Red Clover, as well as Black Knapweed (*Centaurea nigra*) and Bugle (*Ajuga reptans*). The main flowering period in the meadows only began in late June and they were cut for hay in mid-July, truncating the flowering season. As a result, few bumblebees were observed on the meadows except during the early part of July. One of the meadows (section 2: Tables 1 and 2) was included as it was split by a ditch in which there was an abundance of Yellow Flag (*Iris pseudacorus*) flowering in late May and June. Roadsides and path verges were included as connecting sections and also to assess whether such features were likely to be useful across the wider Levels, outside areas in conservation management. Forage species in evidence here included Comfrey and Bramble.

At Ham Wall NNR the area investigated incorporated paths on the banks of the South Drain as well as those bordering some of the reed-beds developed by the Royal Society for the Protection of Birds (RSPB) on the abandoned peat workings. Some of these paths had been seeded with pollen and nectar mixes, including Red and White Clover, in an effort to create forage for scarce bumblebee species. Additionally, some reed-bed and ditch borders provided good quantities of suitable forage for bumblebees such as Tufted Vetch (*Vicia cracca*), Comfrey and Bramble.

The Westhay study site included an area of cut-over, degraded mire dominated by Purple Moor-grass (*Molinia caerulea*) and now being managed as a nature reserve by the Somerset Wildlife Trust, along with some adjacent paths and droves; it was appreciably shorter than the other two transects walked. Few bumblebees were recorded on the mire itself as the main flowering period there fell after the survey period. More bumblebees were observed on the drove leading from the site car park to the core of the reserve, and along the tracks through the reserve bordering the reed-beds; forage sources here included White Dead-nettle (*Lamium album*), Tufted Vetch and Bramble.

For site maps and transect locations see Iles 2010.

Field work techniques

Fixed transects were established on each site using the methodology devised for butterfly-monitoring transects by Pollard (1977). Transects were walked on at least alternate weeks, and weekly where possible, from early May to the end of July 2010. All bumblebees observed were identified to species and caste; also recorded were the plant species from which they were foraging, and whether the bees were nectaring or gathering pollen. Although many bees were observed carrying pollen in their corbiculae (pollen baskets), they were only recorded as pollen-foraging if observed in the act of combing pollen into the corbiculae. The reason for this was that bumblebees can forage from a number of plant species per foraging trip (Heinrich 1979), and in the present study were occasionally observed doing so, and it was therefore unsafe to assume that pollen being carried had come from the species on which they were observed foraging.

Bumblebees not observed foraging have been excluded from the analysis. Those very few individuals seen to be foraging from two species of plant appear in the analysis twice, with a record against each of the plant species concerned.

Identification

Plants were identified using Rose and O'Reilly (2006) and bumblebees determined using Edwards

and Jenner (2004), which as far as possible were identified to caste and to species, except as below:

Workers of *B. lucorum* and *B. terrestris* cannot be distinguished reliably in the field, and have been aggregated together as '*B. lucorum/terrestris*'. Whilst queens and males of these species can be, and were, reliably distinguished, these were observed in relatively small numbers and so have also been aggregated together.

B. humilis, *B. muscorum* and light forms of *B. pascuorum* cannot be reliably distinguished in the field without capture of the bee (Goulson and Darvill 2004; Williams 2009) which was usually not practical on the study sites as the bees were often in the presence of bramble thickets, drainage ditches or open water. These bees were therefore aggregated together as '*B. muscorum* agg'. However, identifiable examples of *B. pascuorum* (dark hairs) were recorded separately as that species, and there were more records of definitely identified *B. pascuorum* than of any other bumblebee recorded in the survey. *B. pascuorum* is ubiquitous, while *B. muscorum* is well known as occurring on the Somerset Levels (Benton 2006; Williams 2009) and also nearby on the Mendip Hills (Saunders 2008). *B. humilis* has been expanding its range and recently reappeared in Somerset (Williams 2009) and, although I cannot trace any definite records of this species from the study areas, its presence cannot be ruled out. The foraging preferences of bees recorded as *B. pascuorum* and *B. muscorum* agg. were different (see below), suggesting that most bees recorded as '*B. muscorum* agg.' were, indeed, *B. muscorum*.

Interpretation techniques

Breakdowns of foraging numbers were made by transect section, habitat type and forage source. The breakdown by transect section was made to examine whether the bees were evenly distributed across the sites, or were clustered in particular sections. The breakdown by habitat type was made to see if any clustering was linked to habitat. For this purpose, each transect section was assigned to one of the following three habitats: drove, verge and meadow (Table 1). The first two are 'edge' habitats alongside paths or roads. Verge habitats were distinguished by being managed for access – either made roads, cycle paths (Ham Wall section 1 and part of section 3) or broad banks alongside large drainage ditches managed for pedestrian access.

TABLE 1: HABITAT TYPE OF EACH TRANSECT SECTION

Transect section	Habitat	Length(m)
Ham Wall 1	Verge	700
Ham Wall 2	Drove	1600
Ham Wall 3	Drove and Verge	600
Ham Wall 4	Verge	500
Ham Wall 5	Drove	500
Ham Wall 6	Drove	450
Ham Wall 7	Verge	1100
Shapwick 1	Verge	1000
Shapwick 2	Meadow	300
Shapwick 3	Meadow	500
Shapwick 4	Meadow	300
Shapwick 5	Meadow	900
Shapwick 6	Meadow	500
Shapwick 7	Verge	1250
Shapwick 8	Meadow	300
Shapwick 9	Verge	500
Shapwick 10	Verge	350
Westhay 1	Verge	300
Westhay 2	Drove	500
Westhay 3	Meadow	300
Westhay 4	Meadow	200
Westhay 5	Meadow	400
Westhay 6	Drove	300

Strictly speaking, a 'drove' is a track across the moors used for driving cattle; here it is used for tracks amongst the reed-beds, typically with extensive and floristically rich hedgerows on either side, beyond which are the reed-beds themselves. The drove sections at Ham Wall had been seeded with pollen and nectar mixes to encourage bumblebees; large amounts of White Clover had established as a result. 'Meadow' habitats comprised areas of open land; the Shapwick meadow sections were hay meadows of varying size (and one, section 6, was rough pasture) whilst the Westhay 'meadow' sections were mostly areas of remnant mire.

Analysis was also made of the forage sources used, both amongst all bumblebees and for different species. In addition to straightforward breakdowns by species, chi-squared tests were performed to test for associations between forage source and tongue length and to determine whether certain forage sources were being used by specific communities of bumblebees.

RESULTS

A total of 786 observations of individual bees foraging were made, involving bees of eleven species (including both *B. lucorum* and *B. terrestris*) (Table 2): the common and widespread 'big six', three cuckoo-bees, *B. vestalis* (Vestal Cuckoo-bee), *B. campestris* (Field Cuckoo-bee) and *B. rupestris* (Red-tailed Cuckoo-bee), the rare *B. muscorum*, and the recent colonist *B. hypnorum* (Tree Bumblebee). The most abundant bees were *B. pascuorum*, *B. lucorum/terrestris*, and *B. muscorum* agg. *B. hypnorum* and the cuckoo-bees were present in very low numbers and, disappointingly, *B. sylvarum* was not recorded at all.

Although the study did not attempt to assess this, it was notable that bumblebees were concentrated on large, tightly-clustered patches of forage – most commonly large patches of Bramble, but also two closely-grouped, large (*c*. 50m^2) aggregations of Tufted Vetch and Narrow-leaved Everlasting-pea (*Lathyrus sylvestris*) on Ham Wall section 6 and Shapwick Heath section 9 respectively. *Thoracobombus* species, especially *B. muscorum* agg., were found infrequently on the scattered Tufted Vetch inflorescences on Ham Wall sections 2 and 3, but were extremely common on the locally abundant patches of Tufted Vetch on Ham Wall section 6, as borne out by the figures in Table 2.

Very low numbers of bumblebees were recorded on the Westhay transect's mire sections, where few flowers were available until the final weeks of the survey.

An examination was made of the associations of species with habitat (Table 3). A chi-squared test was carried out, excluding the cuckoo-bees and *B.*

TABLE 2: FORAGE VISITS OBSERVED, BY TRANSECT SECTION

Transect section	**camp**	**hort**	**hyp**	**lap**	**luc/ terr**	**musc agg**	**pasc**	**prat**	**rup**	**ves**	**Total**
Ham Wall 1	1	3	2	5	17	3	22	16	–	2	71
Ham Wall 2	1	14	3	17	22	11	25	15	–	2	110
Ham Wall 3	–	3	–	1	20	6	8	3	–	1	42
Ham Wall 4	–	1	–	1	1	–	3	–	–	–	6
Ham Wall 5	–	–	–	11	23	3	5	7	–	3	52
Ham Wall 6	–	2	3	2	4	50	26	5	–	–	92
Ham Wall 7	–	1	1	4	16	4	9	1	–	2	38
Shapwick 1	–	3	2	2	10	2	3	3	–	3	28
Shapwick 2	–	6	–	3	3	1	11	1	–	3	28
Shapwick 3	–	2	1	5	5	2	6	–	–	4	25
Shapwick 4	–	–	–	–	3	–	–	1	–	4	8
Shapwick 5	–	3	–	16	1	2	2	1	–	–	25
Shapwick 6	–	3	1	9	4	–	6	4	–	–	27
Shapwick 7	–	–	–	–	3	3	8	2	–	–	16
Shapwick 8	–	2	–	2	1	–	1	–	–	2	8
Shapwick 9	1	1	–	1	14	44	25	13	–	–	99
Shapwick 10	–	1	–	1	5	–	–	1	–	1	9
Westhay 1	–	–	–	4	7	2	25	6	–	–	44
Westhay 2	–	1	–	–	1	2	16	16	1	1	38
Westhay 3	–	1	–	–	4	–	–	–	–	–	5
Westhay 4	1	–	–	1	3	–	1	–	–	–	6
Westhay 5	–	6	–	–	–	1	–	–	2	–	9
Westhay 6	–	–	–	–	–	–	–	–	–	–	0
Total	4	53	13	85	167	136	202	95	3	28	786

Bee species: camp = *B. campestris*; hort = *B. hortorum*; hyp = *B. hypnorum*; lap = *B. lapidarius*; luc/terr = *B. lucorum/terrestris*; musc agg = *B. muscorum* agg.; pasc = *B. pascuorum*; prat = *B. pratorum*; rup = *B. rupestris*; ves = *B. vestalis*

TABLE 3: OCCURRENCE OF BUMBLEBEE SPECIES BY HABITAT

Species	Drove	Meadow	Verge	Total
campestris	1	1	2	4
hortorum	17	23	10	50
hypnorum	6	2	5	13
lapidarius	30	36	18	84
lucorum/ terrestris	50	24	73	147
muscorum agg	66	6	58	130
pascuorum	72	27	95	194
pratorum	43	7	42	92
rupestris	1	2		3
vestalis	6	13	8	27
Total	292	141	311	744

hypnorum due to the low number of records of these species. The test gave a result of $p<0.001$, demonstrating statistically significant associations between species and habitat. This appears to be mainly due to 'under-use' of the meadow areas in comparison with the droves (Table 3). The meadows at Shapwick Heath were cut in mid-July just as potential forage species were coming into flower; as a result, bumblebees which had just begun to use the meadows in numbers soon deserted them altogether. However, the results were still statistically significant even if the meadow data were removed from the analysis ($p<0.001$), with bumblebees preferentially foraging from the droves.

Too few records were made of bumblebees foraging for pollen for an assessment to be made of whether bumblebees were visiting plant species for pollen or nectar.

Bumblebees were observed visiting 36 plant species. Only 15 of these species were visited more than ten times (Table 4), and the three most popular species accounted for almost half of all visits recorded. The 36 plant species (listed in full in Table 7) were from 15 plant families, of which seven were visited on less than four occasions; 85% of plants visited were from four families: Asteraceae, Boraginaceae, Fabaceae and Rosaceae (rose family). This aggregation of data, however, conceals considerable variation in forage use over time. The much larger numbers of workers foraging in July result in higher numbers of observations for plants flowering at that time, whereas early-flowering forage sources vital for establishing nests in May will have fewer recorded visits as there are far fewer bumblebees on the wing then. The forage resources used in May are shown in Table 5.

Visits to forage sources were also analysed according to whether the bees concerned were long-tongued or short-tongued species. The number of visits recorded for each group was broadly similar, but there were clear differences in the plant species visited (Table 6). Particularly noticeable were the results

TABLE 4: FORAGE SOURCES USED BY BUMBLEBEES ON THE TRANSECTS*

Species	Visits	% of total	Cumulative %
Bramble *Rubus fruticosus* agg. (Rosaceae)	204	25.95	25.95
Tufted vetch *Vicia cracca* (Fabaceae)	93	11.83	37.79
Narrow-leaved everlasting-pea *Lathyrus sylvestris* (Fabaceae)	86	10.94	48.73
Comfrey *Symphytum officinale* (Boraginaceae)	73	9.29	58.02
White clover *Trifolium repens* (Fabaceae)	57	7.25	65.27
Creeping thistle *Cirsium arvense* (Asteraceae)	48	6.11	71.37
Yellow flag *Iris pseudacorus* (Iridaceae)	27	3.44	74.81
Marsh thistle *Cirsium palustre* (Asteraceae)	23	2.93	77.74
White dead-nettle *Lamium album* (Lamiaceae)	21	2.67	80.41
Red clover *Trifolium pratense* (Fabaceae)	18	2.29	82.70
Marsh woundwort *Stachys palustris* (Lamiaceae)	17	2.16	84.86
Hedge bindweed *Calystegia sepium* (Convolvulaceae)	16	2.04	86.90
Hemp-agrimony *Eupatorium cannabinum* (Asteraceae)	16	2.04	88.93
Black knapweed *Centaurea nigra* (Asteraceae)	12	1.53	90.46
Spear thistle *Cirsium vulgare* (Asteraceae)	11	1.40	91.86

*Restricted to forage source species with greater than ten visits. Species listed in order of number of visits recorded

TABLE 5: FORAGING OBSERVATIONS, MAY ONLY (ALL RECORDS)

Species	hort	hyp	lap	musc agg	pasc	prat	terr	ves	Total
Bramble *Rubus fruticosus* agg. (Rosaceae)					1	5			6
Comfrey *Symphytum officinale* (Boraginaceae)	6	2		1	12	15			36
White clover *Trifolium repens* (Fabaceae)					1				1
White dead-nettle *Lamium album* (Lamiaceae)	3	1			10	5			19
Yellow flag *Iris pseudacorus* (Iridaceae)	4				4		2		10
Other species		1	1	1				1	1
Total	13	4	1	2	28	25	2	1	76

Bee species: abbreviations as in Table 2

for the Fabaceae which, except for White Clover, were visited far more by long-tongued bumblebees than short-tongued bumblebees. Short-tongued bumblebees displayed a preference for Bramble and thistle species. A chi-squared test established that associations between forage sources and tongue length were statistically significant ($p<0.001$). A similar analysis was carried out splitting bumblebees into sub-genus *Thoracobombus* bumblebees and 'the rest', with broadly similar patterns of association and a statistically significant result ($p<0.001$).

Observations of individual bumblebee species indicate a degree of partitioning of foraging resources between them (Table 7). For example, Bramble was exploited predominantly by the short-tongued *B. lucorum/terrestris* and *B. pratorum*, whilst Tufted Vetch and Narrow-leaved Everlasting-pea were used mainly by *B. muscorum* agg. and *B. pascuorum*. However, other significant forage resources were used by a range of species. The two main visitors to Comfrey were the long-tongued *B. pascuorum* and the short-tongued *B. pratorum*, while *B. pascuorum* and the short-tongued *B. lapidarius* were the main foragers on White Clover.

An analysis of bumblebee foraging visits showed that two, *B. muscorum* agg. and *B. lucorum/terrestris*, had particularly narrow diets. *B. muscorum* agg. foraged predominantly from Tufted Vetch and Narrow-leaved Everlasting-pea, whilst *B. lucorum/terrestris* used mainly Bramble (Fig. 1). This last finding was surprising given that *B. terrestris*, especially, is known to forage from a wide range of food sources (Goulson 2010); an explanation may be that Bramble was highly abundant on the study

TABLE 6: FORAGE SOURCES USED BY LONG-TONGUED AND SHORT-TONGUED BUMBLEBEES*

Species	Long-tongued	Short-tongued	Total
Bramble *Rubus fruticosus* agg. (Rosaceae)	31	173	204
Comfrey *Symphytum officinale* (Boraginaceae)	46	27	73
Creeping thistle *Cirsium arvense* (Asteraceae)	8	40	48
Hedge bindweed *Calystegia sepium* (Convolvulaceae)	13	3	16
Hemp-agrimony *Eupatorium cannabinum* (Asteraceae)	0	16	16
Marsh thistle *Cirsium palustre* (Asteraceae)	8	15	23
Marsh woundwort *Stachys palustris* (Lamiaceae)	17	0	17
Narrow-leaved everlasting-pea *Lathyrus sylvestris* (Fabaceae)	66	20	86
Red clover *Trifolium pratense* (Fabaceae)	17	1	18
Tufted vetch *Vicia cracca* (Fabaceae)	92	1	93
White clover *Trifolium repens* (Fabaceae)	25	32	57
White dead-nettle *Lamium album* (Lamiaceae)	13	8	21
Yellow flag *Iris pseudacorus* (Iridaceae)	23	4	27
Total	359	340	699

* Records presented here are restricted to those plant species which were observed being used as forage sources on more than 15 occasions

TABLE 7: FORAGE SOURCES USED BY INDIVIDUAL SPECIES OF BUMBLEBEE

Total observations	Species										
Forage source	camp	hort	hyp	lap	luc/terr	musc agg	pasc	prat	rup	ves	All
Betony (Stachys officinalis)						1					1
Bird's foot trefoil (Lotus corniculatus)				4							4
Black knapweed (Centaurea nigra)				8	1	2		1			12
Bramble (Rubus fruticosus agg.)	1	2	8	10	96	7	22	41	2	15	204
Bugle (Ajuga reptans)						1				1	2
Comfrey (Symphytum officinale)		11	3	1	5	4	31	18			73
Creeping thistle (Cirsium arvense)	1			4	23	2	6	8		4	48
Eyebright (Euphrasia officinalis agg.)							1				1
Foxglove (Digitalis purpurea)		6				1			1		8
Great bird's foot trefoil (Lotus pedunculatus)				4		1	1				6
Great willowherb (Epilobium hirsutum)					1					1	2
Hedge bindweed (Calystegia sepium)		6			2	2	5	1			16
Hedge woundwort (Stachys sylvatica)							1				1
Hemp-agrimony (Eupatorium cannabinum)				1	11			1		3	16
Honeysuckle (Lonicera periclymenum)		1									1
Lesser burdock (Arctium minus)				2	1	3	3				9
Marsh thistle (Cirsium palustre)		1		5	2		7	4		3	22
Marsh woundwort (Stachys palustris)		1				2	14				17
Meadow vetchling (Lathyrus pratensis)							1				1
Narrow-leaved everlasting-pea (Lathyrus sylvestris)					9	43	23	11			86
Purple loosestrife (Lythrum salicaria)	1				3						4
Rape (Brassica napus)				1							1
Red clover (Trifolium pratense)		3		1		4	10				18
Rosebay willowherb (Chamerion angustifolium)								1			1
Rough hawkbit (Leontodon hispidus)				6				1			7
Spear thistle (Cirsium vulgare)	1	1		4	2		2			1	11
Tormentil (Potentilla erecta)				3							3
Tufted vetch (Vicia cracca)		4			1	56	32				93
Water chickweed (Myosoton aquaticum)								1			1
Welted thistle (Carduus acanthoides)				1							1
White clover (Trifolium repens)		1		25	7	6	18				57
White dead-nettle (Lamium album)		3	1				10	7			21
Woody nightshade (Solanum dulcamara)			1		1						2
Yellow flag (Iris pseudacorus)		9		2	2	1	13				27
Yellow Loosestrife (Lysimacha vulgaris)							1				1
Yellow rattle (Rhinanthus minor)		4		3			1				8
All	4	53	13	85	167	136	202	95	3	28	786

Bee species: abbreviations as in Table 2

area and may have been sufficient to fulfil the needs of the local *B. lucorum/terrestris* population. In contrast, *B. pascuorum*, the close relative of *B. muscorum* agg., appears to have a remarkably broad diet.

Bumblebee diet was also analysed by plant family. This confirmed the reliance of *B. muscorum* agg. and *B. lucorum/terrestris* on a narrow diet, while *B. pascuorum* forages across a wide range of species but displays a strong preference for plants belonging to the family Fabaceae. *B. hortorum*, the least recorded of the 'big six', seems to forage from a remarkably broad range of plant families.

DISCUSSION

Findings of the present study

The major forage sources used by bumblebees on the study sites are summarised in Table 4, while the breakdown of these by the bumblebee species using them is given in Table 7. Just four plant species – Bramble, Tufted Vetch, Narrow-leaved Everlasting-pea and Comfrey – accounted for 58% of the observed bee/plant interactions (Table 4). Numbers of bumblebee workers increased as the survey went on, corresponding with the flowering of the first three

Fig. 1 Bombus lucorum/terrestris *worker foraging on Bramble* (Rubus fruticosus *agg*.)

of these species. However, early in the survey in May, bumblebees foraged from Comfrey and White Dead-nettle, and a little later from Yellow Flag and clovers (Table 5).

Early-emerging habitat generalists can flourish because the hedgerow and ditch-bank vegetation has plenty of early-season forage: Goat Willow (*Salix caprea*), Sallow (*S. cinerea*), White Dead-nettle and Comfrey. These bumblebees are then able to shift their attention to grassland areas when these begin to come into flower. However, early mowing of meadows on the Levels – the Shapwick meadows were mowed later than most, yet were still mowed earlier than ideal for bumblebees – meant that bumblebees had few opportunities to forage from grassland during the study period, but the seeded areas of drove at Ham Wall held meadow Fabaceae such as clovers and Bird's-foot-trefoil that were used widely by *B. pascuorum* and *B. lapidarius*.

During July, two small flower-rich patches of forage, of Tufted Vetch on Ham Wall section 6 and of Narrow-leaved Everlasting-pea on Shapwick section 9, attracted good numbers of *Thoracobombus*, especially *B. muscorum* agg. More generally, there were concentrations of bumblebees around large clumps of Bramble. Although not investigated by the survey, there appeared to be an association between concentrations of bumblebees and concentrated sources of forage.

The most significant bumblebee observed, in a national context, was *B. muscorum*. Identification difficulties make interpretation of its foraging habits only tentative, but it did appear that this species was foraging to a high degree (81%) from Tufted Vetch and Narrow-leaved Everlasting-pea, and some of the other observations (five of seven visits to Bramble, for example) were of males that do not forage for the nest. Interestingly, among the few observations of pollen-gathering, eight of 22 featured *B. muscorum* agg. using these Fabaceae. However, few observations were made of *B. muscorum* agg. early in the study when colonies were being established and Fabaceae were not in flower; in these instances Comfrey (twice), Yellow Flag, Foxglove and Bugle (*Ajuga reptans*) were the species visited. Concentration on its key forage plants occurred from mid-July onwards: in late June and early July, 23 bees were noted foraging from nine different species, whereas, later in July, 91 of 110 visits recorded were to Tufted Vetch and Narrow-leaved Everlasting-Pea.

B. hortorum used a wide range of forage sources, with no plant family accounting for more than 25% of observations and five families in the range 11–21%. This masks a seasonal variation, however, as its diet was clearly more restricted in spring: 13 records of this species foraging in May involved just three forage sources – Comfrey, Yellow Flag and White Dead-nettle – whereas 14 visits in July involved ten plant species.

Seventy-five per cent of *B. lucorum/terrestris* observations were on Bramble and Asteraceae, and this species-pair had the lowest use of Fabaceae among the common bumblebees recorded. Its early-season forage on the three study sites is unknown; although the second most widely recorded species overall, the only records in May were of two *B. terrestris* queens foraging on Yellow Flag on 31 May. Amongst workers, reliance on Bramble was at its most marked in June (eg 20 June, 40 of 44 workers foraging on bramble); in late July, there was a wider range of potential forage sources (eg 31 July, 15 workers foraging from eight species). Although there were relatively few observations, the foraging patterns of the cuckoo-bee *B. vestalis* appeared similar to that of its host, *B. terrestris*.

Ninety-two per cent of observations of *B. lapidarius* were from three families, Fabaceae, Asteraceae and Rosaceae. Like *B. lucorum/terrestris*, it was not observed until 31 May, although it is an early-emerging species (Benton 2006). Its use of plants varied according to caste (Table 8). Workers foraged from White Clover, Bramble and Black Knapweed, whilst males used several species, principally Asteraceae, not used by the workers.

B. pascuorum, the most commonly observed bumblebee, showed a preference for Fabaceae (42% of observations) but depended on Fabaceae less than its close relative *B. muscorum* agg. and foraged from a wider range of species within this family. In May,

TABLE 8: *BOMBUS LAPIDARIUS* FORAGING VISITS, BY CASTE

	Males	Queens	Workers
Bird's-foot-trefoil *Lotus corniculatus* (Fabaceae)	–	–	4
Black knapweed *Centaurea nigra* (Asteraceae)	1	–	7
Bramble *Rubus fruticosus* agg. (Rosaceae)	2	–	8
Comfrey *Symphytum officinale* (Boraginaceae)	–	–	1
Creeping thistle *Cirsium arvense* (Asteraceae)	4	–	–
Great bird's-foot-trefoil *Lotus pedunculatus* (Fabaceae)	4	–	–
Hemp-agrimony *Eupatorium cannabinum* (Asteraceae)	1	–	–
Lesser burdock *Arctium minus* (Asteraceae)	2	–	–
Marsh thistle *Cirsium palustre* (Asteraceae)	5	–	–
Rape *Brassica napus* (Brassicaceae)	–	–	1
Red clover *Trifolium pratense* (Fabaceae)	–	–	1
Rough hawkbit *Leontodon hispidus* (Asteraceae)	–	–	6
Spear thistle *Cirsium vulgare* (Asteraceae)	1	–	3

queens and workers foraged primarily on Comfrey, White Dead-nettle and Yellow Flag (26 of 28 observations); in June, foraging shifted to clovers and, in July, to Tufted Vetch and Narrow-leaved Everlasting-pea.

B. pratorum also displayed a seasonal pattern. In May and early June it foraged on Comfrey and White Dead-nettle. Later, like *B. lucorum/terrestris,* it moved on to Bramble and thistles (*Cirsium* and *Carduus* spp) and foraged from just one Fabaceae species, Narrow-leaved Everlasting-pea (12% of observations).

Of the non-cuckoo bumblebees the fewest records were of *B. hypnorum*. This species is a recent colonist of the UK, is expanding its range both here and in mainland Europe, and seems to be a generalist species that thrives in proximity to humans (Goulson *et al*. 2006). There are very few previous records in Somerset (S.P. Roberts pers. comm.). It appears to be quite widespread on the Levels and has been recorded twice from Berrow. Numbers recorded were too low for analysis of its forage, though most observations (nine of 13) were on Bramble, with early-season records on Comfrey and White Dead-nettle, in a similar manner to *B. pratorum.* Workers were repeatedly recorded at the same locations on particular sections of the Ham Wall and Shapwick transects, suggesting a very limited number of nests.

To summarise, the key forage sources on the study sites in May were Comfrey, White Dead-nettle and Yellow Flag, which were favoured especially by the long-tongued species. There were surprisingly few records of *B. lucorum/terrestris* and *B. lapidarius*; as these are capable of foraging over longer distances than other bumblebees (Goulson 2010) it is possible that they were finding forage away from the study sites, although I failed to locate them in any numbers in searches elsewhere at this time. Later in the year, *Thoracobombus* species used Fabaceae, especially Tufted Vetch and Narrow-leaved Everlasting-pea, whilst short-tongued bumblebees use Bramble and, to a lesser extent, thistles.

Limitations of the present study

Two significant caveats need to be applied to interpreting the data above. Firstly, the study did not cover the whole time period in which bumblebees would have been foraging; the first visits were on 13 May 2010 and the last on 31 July 2010. The first surveys were timed to capture the emergence of queens of the scarce and late-emerging *Thoracobombus* species. Visits to early-season forage sources were not observed – for example, Sallow, a known early bumblebee forage source, was widespread in the study areas and may have been a key species before Comfrey and White Dead-nettle came into flower. More significantly, owing to the project deadline, foraging in late summer could not be observed, which was unfortunate as the peak flight period of *B. sylvarum* is late August and because declines of some *Thoracobombus* species could be related, in particular, to a shortage of late-season forage.

Secondly, there were difficulties identifying bumblebees to caste. For certain species – *B. lapidarius*, *B. pratorum* and *B. lucorum* – caste is

relatively easy to identify as males show distinctive colour patterns. On the other hand, very low numbers of *B. hortorum* and *B. pascuorum* males were recorded, due no doubt to the fact that males of these species are hard to distinguish in the field – indeed, there is a suspicion that males were repeatedly being misidentified as workers. This is potentially important as males do not collect pollen, and forage only for themselves, playing no part in provisioning the nest. For this reason, with the exception of *B. lapidarius* (Table 8), it was considered inappropriate to interpret the results by caste, analyses instead being carried out on the foraging habits of all bees irrespective of caste.

The numbers of bees recorded do not provide information on the relative abundance of bumblebee species. The typical number of workers per nest varies from species to species, with nests of *B. terrestris* often containing over 200 workers and those of *Thoracobombus* under 100 (Edwards and Jenner 2004); bumblebee population is perhaps best measured in terms of the numbers of colonies (Ellis *et al.* 2006). It is also possible that some species were under-recorded. *B. sylvarum*, for example, tends to fly among rather than above dense foliage, and this habit may make it relatively harder to detect (Benton 2006).

Comparison with other findings

Scarce bumblebees survive across a range of different habitats, such as calcareous grassland, heathland, moorland and wet fen – the common denominator being that all these habitats are rich in suitable forage resources (Goulson *et al*. 2006). On the coast of Cornwall, *B. muscorum* queens are recorded as foraging from Kidney-vetch (*Anthyllis vulneraria*) and workers from Bell Heather (*Erica cinerea*) (Saunders 2008). The single most used nectar source in the national study by Goulson *et al*. (2005) was Viper's Bugloss. The Bumblebee Working Group (2002) reported *B. sylvarum* populations in the south-east using Narrow-leaved Bird's-foot-trefoil (*Lotus glaber*) and Red Bartsia (*Odontites verna*), and Carvell *et al*. (2006) noted it using Black Horehound. None of these species was recorded on any of my study sites although another 'heather', Cross-leaved Heath (*Erica tetralix*), was found to occur on parts of the remnant mire at Westhay. It seems evident that bumblebees, even those species that forage on a particular site from a restricted range of forage sources, can use different plant species in different sites and habitats.

The significance of small concentrated patches of flower-rich forage, observed in the present study for *B. muscorum* agg., has been observed elsewhere. For example, a small patch of Willow (*Salix* sp.) on Dartmoor provided forage that seemed to attract *B. monticola* (Mountain Bumblebee) queens from a wide area (Aculeate Conservation Group 2003). Carvell (2002) noted that 'bumblebee forage use was significantly related to flower abundance' on Salisbury Plain although *B. humilis* appeared to be an exception with a preference for foraging from widespread but sparsely distributed flowers. The concentration of *Thoracobombus* species on large patches of flowering Tufted Vetch, whilst scattered flowering plants of the same species were less utilised, suggests that availability of Tufted Vetch is not limiting population size in these species, but that other factors may be of greater significance in this regard, eg amounts of forage earlier or later in the season, or availability of nest-sites.

The absence of records of *B. sylvarum* in the present study is a source of concern, as information on its foraging habits and habitats would have been of considerable interest, and of relevance to its conservation. Its absence is not altogether surprising, since the survey was carried out prior to the peak flight period for this species (late August) and the population of *B. sylvarum* on the Levels always appears to have been thinly distributed (R. Williams, pers. comm.; P. Rayner, pers. comm.). *B. sylvarum* used to be common and widespread (Sladen 1989), at least in southern England, and remains abundant at some of its British sites (Benton 2006). The Levels may always have been marginal for this species; perhaps, since the area has had relatively limited agricultural change, *B. sylvarum* has been able to persist here for longer than in surrounding areas which may originally have been more suitable for it.

The extensive use of Fabaceae by *B. muscorum* agg. concurs with Goulson *et al*. (2005) and Benton (2006), who find Fabaceae, including Tufted Vetch, are used predominantly – for both nectar and pollen – by *B. muscorum*.

Other potential constraints on bumblebee populations

Shortage of nest sites has been advanced as a possible cause of bumblebee decline (Bumblebee Working Group 2002). *Thoracobombus* bees use disused small mammal nests at or slightly above ground level and seem to prefer grassland with an open structure

rather than tussocky grassland, presumably because the nest can be warmed by the sun in open grassland. *B. humilis, B. sylvarum* and *B. muscorum* require tall grassland with plenty of leaf litter or moss for them to use as nesting material (Bumblebee Working Group 2002; Edwards and Jenner 2004), although *B. pascuorum* appears to be more flexible in its requirements (Benton 2006). *B. muscorum*, which has a more northerly range, appears to tolerate denser (and therefore cooler) grasslands than *B. sylvarum* or *B. humilis* (Benton 2006). This is interesting in the context of the present study, as grassland on the Levels is generally fairly dense, and the area tends to experience cool winters and springs, being described as a large frost-pocket (Whitefield 2009). This may explain the absence of *B. humilis*, and why *B. muscorum* is relatively common on the Levels in comparison with *B. sylvarum*.

The Bumblebee Working Group (2002) noted that the nests of *B. muscorum* and *B. humilis* are prone to destruction when hay is cut, but this is unlikely to have contributed to any recent decline as, where hay meadows have survived, cutting times have remained largely unchanged (P.Rayner, pers. comm.). However, amending cutting practice on hay meadows might afford opportunities for furthering the conservation of bumblebees; if some areas are not cut every year, this would allow nests to remain undisturbed when the rest of the meadows are being cut; additionally, uncut areas would provide suitable habitat for small mammals (Bumblebee Working Group 2002; P.Rayner, pers. comm.), thereby potentially increasing the number of old nests that would provide suitable nesting sites for *Thoracobombus* species, as well as extending the period during which these meadows could provide useful pollen and nectar sources.

CONCLUSIONS

Key findings

On the Somerset Levels, bumblebees appear to exploit a relatively narrow range of forage sources. These change according to the season: in late spring, Comfrey, White Dead-nettle and Yellow Flag are the key species, whilst in high summer, Bramble, Tufted Vetch and Narrow-leaved Everlasting-pea are the species most used. Maintaining and enhancing populations of these key forage species ought to provide sufficient forage to conserve the area's bumblebee populations, the caveats being that late summer forage sources (which might limit bumblebee populations) have not been studied, and that no observations were made of the most significant species, *B. sylvarum*. On the study sites the other nationally scarce species, *B. muscorum*, appears to benefit in high summer from two small, highly concentrated flower-rich patches of Fabaceae (Tufted Vetch and Narrow-leaved Everlasting-pea).

Suggestions for management

Conservation of the two patches of Fabaceae heavily used by *B. muscorum* and the replication of these patches elsewhere within the study sites, if not more widely across the Levels, is an obvious course of action. Possible locations might include, for Tufted Vetch, the drove forming Westhay sections 1 and 6 and hedgerow and bankside locations on Ham Wall sections 4 and 7; and, for Narrow-leaved Everlasting-pea, locations along the South Drain similar to that on Shapwick section 9, parts of Ham Wall sections 1 and 3, unwalked bankside sections of Shapwick Heath, and parts of the car park bank at Westhay. Conserving these plants may also be of benefit to *B. sylvarum,* for which these are known to be important food sources on the Newport Levels (Lee 2009).

Early-season and late-season forage should also be conserved. For early-season forage, this would entail hedgerow and bank-side management for Comfrey and White Dead-nettle, and ditch management to encourage large stands of Yellow Flag similar to that on Shapwick section 2.

More widely, encouraging bumblebee-friendly land management through agri-environment schemes needs to continue. Ditch management might encourage Yellow Flag, whilst crops of Red Clover might be encouraged – a field of Red Clover near Meare, not far from the Ham Wall study area, was the only one observed during the survey.

Suggestions for future research

There are two interlinked priorities for further research on the bumblebee populations of the Somerset Levels: first, to establish which plant species are important foraging sources in late summer; and second, to establish where *B. sylvarum* still occurs and to ascertain which plant species are important as sources of nectar and pollen for that species.

Further investigation of the foraging preferences of queen *B. muscorum* would also be of value, so

that measures can be taken to safeguard and/or enhance its early-season forage sources.

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