# *Bombus ruderarius* (Müller, 1776): Current knowledge of its autecology and reasons for decline

**Ted Benton**

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**Hymettus Ltd., Lea-Side, Carron Lane, MIDHURST, West Sussex GU29 9LB**
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Cover photograph:
*Bombus ruderarius* queen by Ted Benton

# Summary

- There is some uncertainty in interpreting distribution maps, especially for earlier periods, due to the difficulties encountered by many observers in confidently identifying individuals of this species (especially the worker caste) in the field. However, there is little doubt that *Bombus ruderarius* is a rapidly declining species both in the UK and in large parts of central, western and northern Europe. Formerly it was widespread in the UK, but with a strong bias toward the south-east.

- In the UK and elsewhere in Europe, the bee is found in a wide range of habitats: open, flower-rich (especially calcareous) grasslands, coastal dunes, wetlands, grazing marshes and sea-defences, less intensively managed farmland, and urban/ suburban brown-field sites, ruderal habitats and gardens. Toward the southern edge of its range in Europe it may sometimes be common in a variety of grassland and forest-edge habitats in mountains.

- Nesting habitat is generally in tall, tussocky grassland, often close to scrub or woodland edge. The nest is usually on the surface or just below, made of grass-clippings and mosses, and often founded on an old mouse or vole nest.

- Nests are small in size, and it seems likely that at maturity the number of workers is small compared with many other UK species (possibly 20-50 individuals).

- Queens emerge from hibernation a little later than species such as *B. terrestris, B. pratorum*, and *B. pascuorum* (though some authors say it flies earlier than *pascuorum*), in early April (somewhat later in ‘late’ localities), but earlier than the other scarce ‘carder’ bumblebees (*B. sylvarum, B. muscorum, B. ruderarius*). The colony cycle is short, with males and young queens emerging from early July onwards.

- There is some evidence that *ruderarius* is especially generalist in its use of forage sources (Iserbyt, Durieux & Rasmont’s (2008) study supports the conclusions of Goulson *et al.* (2005) in this respect). However, most data sets so far do not discriminate between nectar and pollen collection. Such evidence as is available suggests a strong reliance on a range of species in the families Scrophulariaceae, Fabaceae, and Lamiaceae for pollen. *B. ruderarius* is usually classified as a medium tongue-length species.

- With a small number of exceptions, *B. ruderarius* appears to be one of the scarcest species of bumblebees wherever it occurs in the UK. The known exceptions are sand-dune habitats at Shoreham in the early 1980s, and on the machair at Tiree. In southern Europe, it is one of the commonest species in the rich bumblebee community of the Pyrennean Eyne valley. However, in other bumblebee communities studied in mainland Europe, *B. ruderarius* is generally among the least abundant and more localised species.

- Little is known about the vulnerability of *B. ruderarius* to predators and parasites, though Sladen (1912) noted its vulnerability to wax-moth infestations.

- The species has a wide geographical distribution from north to south in Europe, and this may also reflect a wide climatic range, given its presence through an upper altitudinal range of more than 1200m in the Pyrenees (sites below 1480m were not studied).

# Contents

# 1. Distribution and Status

## 1.1 UK distribution and status

For early writers, *Bombus ruderarius* was considered widespread, common and often abundant. For example: ‘It is more plentiful in some localities than in others, but it may be looked for in all parts of the country’ (Step, 1932, p.9); ‘Normally an abundant species from north to south, including Ireland’ (Free & Butler, 1959, p.187; ‘..a widely-distributed species in Great Britain and Ireland, and common in many places, especially in the north of England’ (Sladen, 1912, p.189); ‘Common and generally distributed’ (Saunders, 1896). Comments by these authors on its UK distribution suggest that it may once have had a more extensive presence in the north than is indicated by later distribution maps. According to Alford (1975) it was ‘a widespread species…often common in the south and south-east of England, ..but

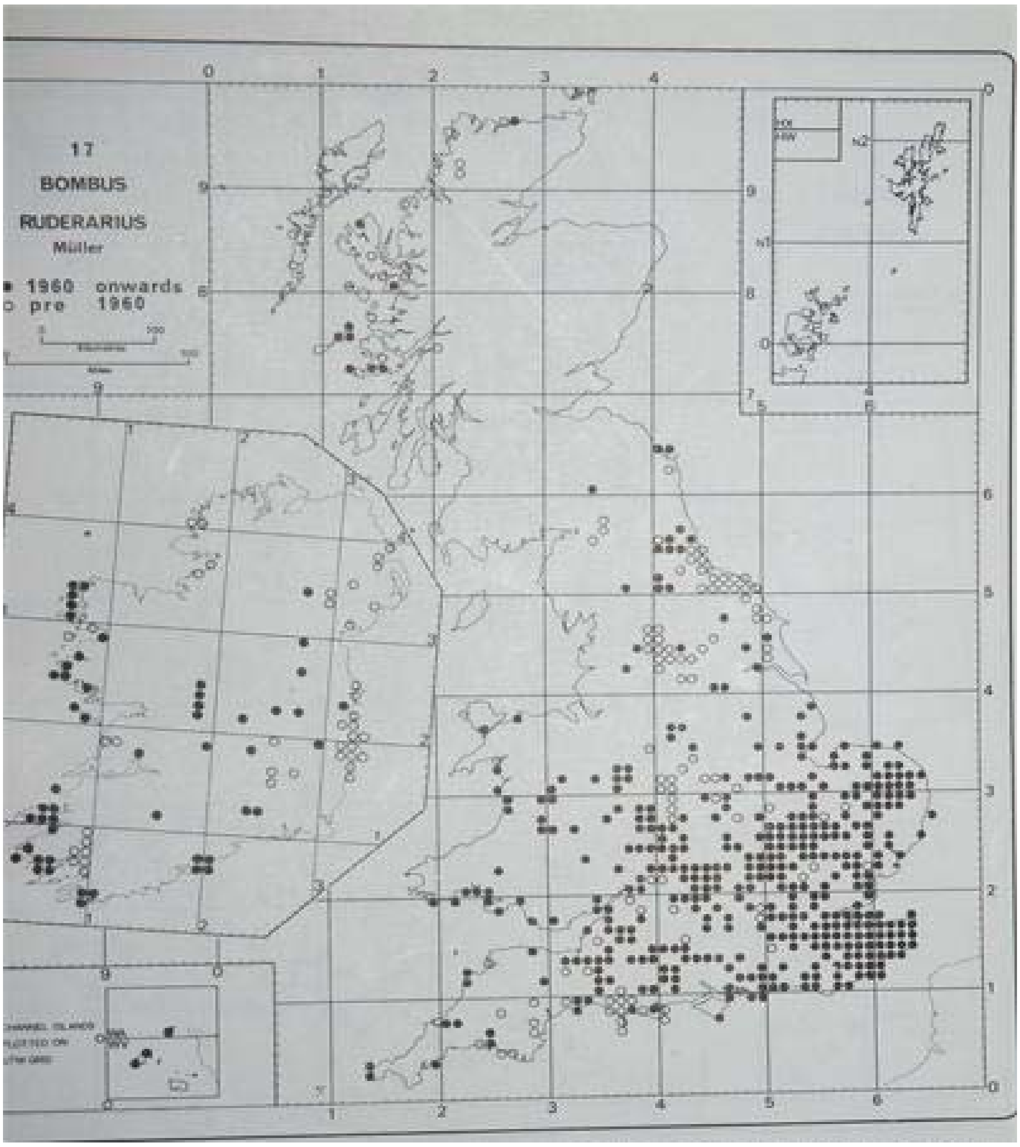

Figure 1: Distribution map for *Bombus ruderarius* from 1980 ITE bumblebee atlas

scarce or absent in many parts of the country'. The ITE Atlas (Anon., 1980) also gives a UK distribution strongly skewed to the south-east of England, with increasingly patchy and dispersed records towards the north and west (see Fig.1).

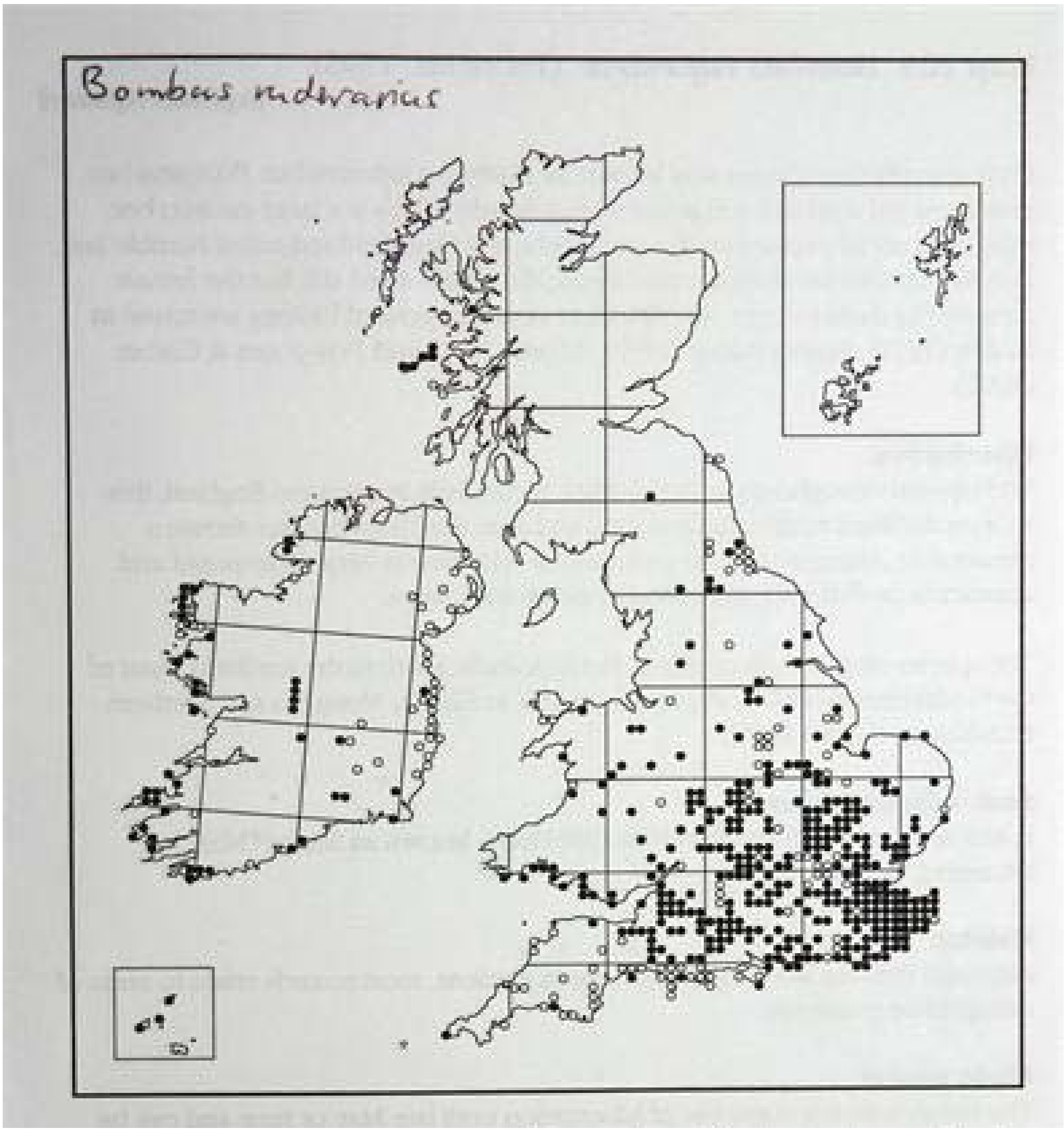

Figure 2: Distribution map for *Bombus ruderarius* from 2001 BWARS atlas showing pre-1970 records as open circles o and post-1970 records as solid dots ●

Comparison of the distribution prior to 1960 with that from 1960 onwards indicates significant decline in the south-west and north of England and the eastern coastal districts of Ireland. Figure 2 showing the more reliable distribution map given in the BWARS Atlas 3 (Edwards & Philp, 2001), enables comparison between pre-1970 and 1970 onwards date classes, omitting unverified earlier records. Here, however, the pattern remains quite similar, with densest distribution in the extreme south-east of England, more patchy distribution to the north and west, and only scattered localities inland in Ireland, the midlands, East Anglia and northern England. This map shows significant losses from 1970 onwards in the south-west peninsula and north-east England and the east coast of Ireland. However, the species remained well distributed along the west coast of Ireland, south coast of Wales, and maintained its presence in the Inner Hebrides.

## 1.2 Global Distribution and Status

In the rest of Europe, the species ranges from the Mediterranean, in the south, northwards to approximately 66° in Sweden and 64 ° in Finland. Eastwards its distribution includes Turkey, the Caucasus, the southern part of Western Siberia, northern Kazakhstan and Baykal (Løken, 1973) (see Figure 3). However, since the source for this was published in 1973, its current geographical range may be rather different. There is evidence of recent decline in mainland Europe as well as UK e.g. in Baden-Wurtenberg where it is rare (Westrich, P. via Edwards, M., 2008). In southern Germany it was reported to be the scarcest of the carder bees, one queen only being recorded on a study-trip in May 2001 (Edwards, 2001). In Switzerland it was formerly widespread especially in the south, but localised. The 1996 distribution map shows significant decline (more than 50%) comparing pre-1970 with 1970 onwards date-classes (Amiet, 1996).

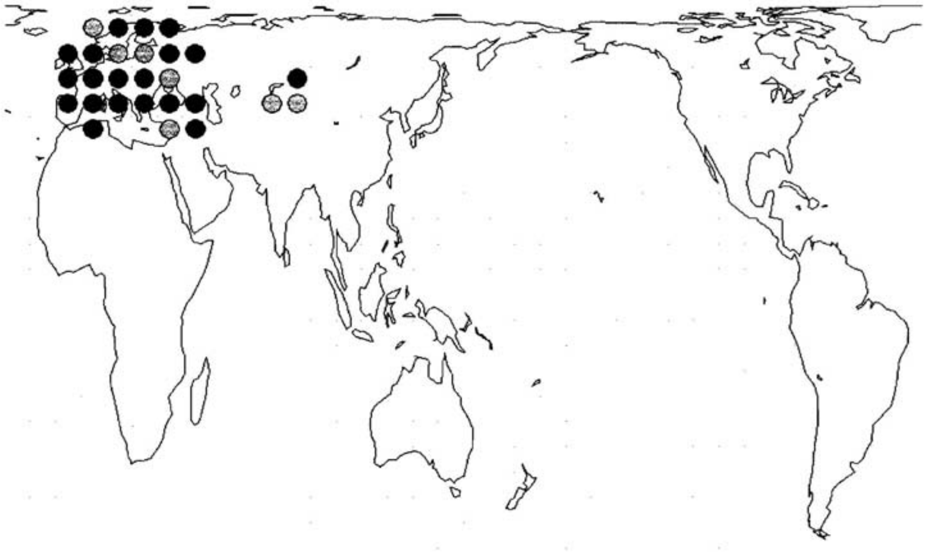

Figure 3: Global distribution of *Bombus ruderarius*. The three detached dots refer to a closely related taxon that may or may not be con-specific with *B. ruderarius*. The map was kindly supplied by Paul H. Williams (NHM).

According to Løken (1973) *B. ruderarius* was widespread in the lowlands of southern Sweden, and in Norway to the south-eastern lowlands and south coastal districts at least until 1973. Rasmont (2008) states that in the vicinity of Uppsala, Sweden, reversion to organic agriculture, with the return of large-scale cultivation of agricultural legumes, such species as *B. ruderarius, B. sylvarum, B. humilis, B. subterraneus* and *B. distinguendus* are to be seen. In Belgium and northern France, *B. ruderarius* is in strong decline, according to Rasmont (2008), but in suitable locations in southern France it may sometimes be abundant (Iserbyt, Durieux & Rasmont, 2008).

# 2 Habitat

## 2.1 UK habitats

In the UK most authors concur on the requirement of *B. ruderarius* for open, flower-rich grassland (Edwards & Williams, 2004; Edwards & Philp, 2001: Baldock, 2008; Pinchen, 2004). Both Baldock (2008) and Pinchen (2004) single out unimproved chalk downland as particularly favoured. Salisbury Plain holds a significant population and Edwards (1999) reports 'several queens' nest-searching on 30th April 1999. However, Edwards (2002) notes that the 2002 survey of 9 sites on Salisbury Plain yielded records of this species in only 4 sample sites (compared with all 9 for *B. humilis*).

Pinchen (2004) also mentions coastal and wetland habitats. *B. ruderarius* is present at Kenfig National Nature Reserve, Glamorgan (Carvell, 2000; Edwards, 2000), a coastal reserve, comprising vegetated dunes and flower-rich grassland. In the early 1980s *B. ruderarius* was one of the most abundant bees noted by Williams on his transects on sand-dunes near Sandwich, and Baldock (2008) mentions a riverside meadow. *B. ruderarius* also occurs in small numbers on grazing marshes and sea-walls where there is an abundance of forage plants. Edwards (1999) noted its presence (with *B. muscorum*) on a 'sympathetically managed' ('intermittently mown') stretch of sea-wall in a Kent Wildlife Trust reserve at Graveney, and also at Elmley, Stodmarsh and Sheppey, in Kent (Edwards, 2002).

Prys-Jones & Corbet (1987) mention gardens, and the presence of the species in urban and suburban habitats is confirmed by Williams (2008), and by my own observations. Williams recalls it as present, but rare in Bromley and Chislehurst on the south-eastern fringe of London from the early 1970s, and still present with no obvious decline. Here it foraged and formed nests in suburban gardens. In Colchester, Essex, *B. ruderarius* is similarly rare, but probably still present in small numbers in a range of urban habitats – over-grown brownfield sites, low-maintenance public open spaces with tussocky grassland and scrub, edges of sports fields and allotments. It also occurred and may still occur on a mosaic of old pasture and ruderal habitat by the river Chelmer on the eastern outskirts of Chelmsford (Benton, T. - personal observation). This site was a large complex including ruderal habitat, formerly arable land, recently acquired for a building project, and a smaller area of former pasture, now not grazed, but cut annually. Both sites had red and white deadnettle in spring, and the former had large stands of black horehound later in the season, together with extensive patches of four species of thistle.

Figure 4: A typical brownfield habitat of *Bombus ruderarius*

Edwards & Philp (2001) suggest that it is able to survive in less intensified agricultural habitats. This is born out by Williams (2008) who found it common in hedgerows on the margins of cereal fields at Shoreham. This is also true of some Essex populations where it is occasionally seen foraging on hedge-banks or track-sides by arable fields, or on small uncultivated patches of tussocky grassland (Benton, T. - personal observation). George Else saw queens and workers most years on farmland at Cholderton, close to Salisbury Plain (Edwards, 2008). As elsewhere, queens were observed prospecting for nest-sites in tussocky grassland. The north-western ‘outlier’ population at Tiree is abundant on the machair grassland – according to Edwards (1999) the most frequently seen species on his visit.

What appears to be currently one of the most stable populations exists on open grassland and wide rides in the East Anglian brecks, in some areas occupying the same territory as the nesting habitat of the stone curlew. Here, however, the workers also forage along a hedge-bank adjacent to an old cart track, as well as on adjacent low-intensity farmland, set-aside and roadside verges.

On one occasion in late May a queen was observed prospecting for nest-sites among coarse, tussocky grass along a hedgerow. Edwards (2000) notes: ‘…surface-nesting species (sub-genus *Thoracobombus*, includes *humilis, muscorum, ruderarius, sylvarum*) use old summer nests of small mammals…Such small mammals are much more plentiful in taller grassland. The structure of the grassland is apparently important, with many surface-nesting bumblebees requiring an open grass structure which allows the sun to warm the top of the nest. Modern agricultural methods have resulted in a large reduction of suitable bumblebee nesting habitat.’

Figure 5: Typical habitat of *Bombus ruderarius* in the Suffolk brecks

## 2.2 Mainland Europe

Here the habitat of *B. ruderarius* is given as open land and 'park-like' landscapes (parkartige Landschafften) in Switzerland, where it occurs in the Jura and Alps up to the tree-line (Amiet, 1996). In Germany it is said to principally inhabit lowlands and open land, fields and parks and gardens. In mountains it is found up to 2200m. It also is found in field-, path- and road-sides, embankments and ditches (von Hagen & Aichorn, 2003). In Germany, as in UK, it nests in tussocky grassland, often in transition to scrub and secondary woodland, but also requires rich forage (Edwards, 2008). According to Løken (1973), in Sweden it nests on the ground in moss and grass in hay fields and pastures, avoiding the wooded hills. In Norway, the habitat inland is given as cultivated fields, meadows and gardens, and also as particularly frequent on sand dunes at Jaeren (cf. Paul William's observations at Sandwich, above, and its presence at Kenfig). Løken (1973) mentions 'Leguminosae fields' – presumably a reference to fallow plantings of agricultural legumes.

A single queen found by Mike Edwards in southern Germany in May 2001 was nest-searching in scrubby woodland edge habitat, apparently a rare habitat in that part of Germany, but more common in the UK, where the decline of the species has come later than appears to have been the case in Germany (Edwards, 2001).

A study of Finnish farmland (Backman & Tiainen, 2002) included *B. ruderarius* as present on field margins, but it was recorded in far lower numbers than almost all other species – only 9 individuals, compared, for example, with 900 *B. terrestris* and 289 *B. lapidarius*. In this and other studies, the difficulty of separating worker *B. lapidarius* and *B. ruderarius* in the field needs to be taken into account. However, a study of the Eyne Valley, in the eastern Pyrenees found it to be widespread at altitudes between 1480m and 2740m but with a bias toward the lower altitudes within this range. In this exceptionally diverse bumblebee community (33 species) *B. ruderarius* was one of the most common species (along with *B. lucorum, B. soroeensis, B. monticola* and *B. pyrenaeus*). Other 'carder' bumblebees that also occur in the UK included *B. humilis* and *B. sylvarum*, which were mostly confined to meadows below 1700m, and *B. pascuorum*, which occurred mainly between 1700m and 2100m. The area is described as traditional mixed farmland, with a mosaic of habitats associated with the different altitudinal levels, and comprising an exceptionally rich floristic diversity. A numerical account of flower visits revealed *B. ruderarius* as the most generalist species, with 57 plant species used, drawn from 16 families. Unlike most other species, floral visits were not concentrated on any species, with red clover (*Trifolium pratense*) and *Rhinanthus pumilus* (Scrophulariacea) at only 12% and 19% of visits respectively being the most popular forage plants. Fabaceae and Lamiaceae species were prominent among the range of species visited, but they were also the most widely represented families among all those visited by bumblebees during the survey. As well as being among the most widely distributed species according to altitude, *B. ruderarius* was also found to be among the least specific as to habitat, being found in a range of meadow and forest edge habitats across the study area.

# 3. Biology

## 3.1 Foraging

Sladen (1912) notes the fondness of queens for the flowers of white deadnettle and also mentions that this species is one of the few that will visit ground ivy (confirmed by George Else, via Edwards, 2008). Alford (1975) simply repeats this, but adds bramble as forage for workers, and states that males are partial to knapweeds (*Centaurea*). Williams (1989) recorded foraging visits to flowers at Dungeness during June-August in 1982 and Shoreham during the same period of 1983. His transect followed vegetated shingle ridges at Dungeness. *Teucrium scorodonia* (wood sage) attracted the most workers at 6, *Lathyrus sylvestris* (narrow-leaved everlasting pea) was next in popularity (just 3), and the rest, *Echium vulgare* (viper's bugloss), *Cirsium vulgare* (spear thistle) and *Rubus fruticosus* (bramble), had just one recorded visit each. At Shoreham the research area was a mixture of wheat fields, woodland and grassland (a golf course). The transect followed woodland and field borders. Despite the poverty of bumblebee species compared with the Dungeness site, more flower-visits by *B. ruderarius* workers were recorded: 22 on a red-flowered labiate (mis-identified as *Lamium purpureum* – probably *Ballota nigra* (black horehound), 6 on *Medicago sativa* (lucerne), 2 on *Convolvulus arvensis* and 1 each on *Dipsacus fullonum* (teasel) and *Trifolium pratense* (red clover). Unfortunately, Williams' data do not discriminate between visits for nectar and for pollen, but the list does suggest a preponderance of visits to flowers with deep corollas, in the families of Lamiaceae and Fabaceae at both localities, despite wide differences in the available forage sources in the two areas.


Figure 6: *Bombus ruderarius* queen foraging on white dead nettle

Between 1980 and 1999 Benton (2000) observed queens, following hibernation, to forage from red and white deadnettle, common vetch and red clover. The association with white deadnettle was especially strong in urban areas, and it was used as a pollen source. Workers visited white deadnettle, too, as well as bird's foot trefoil, comfrey, white clover, mallow, bramble, narrow-leaved bird's-foot trefoil, melilot, dyer's greenweed, red deadnettle red clover and spear thistle. Males were observed on white clover, teasel and black knapweed. Young queens were observed on bird's-foot trefoil.

In their location by the river Chelmer on the outskirts of Chelmsford, queens were observed in the third week of April 2004 collecting pollen from white deadnettle. By the beginning of July workers present at the site were collecting pollen and nectar exclusively from black horehound (but were greatly outnumbered by *B. pascuorum*, *B. lapidarius, B. hortorum, B. terrestris/ lucorum* workers, all using the same forage plants). *B. ruderatus* workers were also present, also collecting nectar and pollen from black horehound, and also in small numbers (Benton, T. - personal observation).

At King's Forest, in the Suffolk brecks, queens have been observed foraging from bird's-foot trefoil and purple milk-vetch in the latter half of May, collecting pollen from the latter (Benton, T. - personal observation, Edwards, M. - personal observation). Both workers and queens were also observed in late May foraging from houndstongue (no pollen loads), and workers, on the same occasion, collecting pollen from purple milk vetch. In June and July workers are seen foraging from black horehound (pollen), viper's bugloss (see Figure 9) and bird's-foot trefoil. Males have been seen here on thistle flower-heads as well as foraging from black horehound (Benton, T. - personal observation).

Figure 7: *Bombus ruderarius* foraging on white clover

Figure 8: Dark form of *Bombus ruderarius* worker

Figure 9: Viper's Bugloss in Suffolk brecks

Such pollen-load samples as I have information on (15) mostly contained Fabaceae pollen (80% - from *Vicia, Lathyrus* and *Trifolium*), with smaller numbers containing pollen from Asteraceae, Rosaceae and Lamiaceae. Some of these loads may have contained pollen from a mixture of sources. One queen observed at Cholderton had pollen from *Prunus* sp. (Edwards, 2008).

## 3.2 Nesting biology

Sladen (1912) took many nests, always on the surface, and frequently in long grass on roadside banks. Step (1932) repeats this. The nest has a roof of shredded grass blades and moss, usually on the surface, but occasionally slightly underground, under cover of tall vegetation, and often in an old mouse-nest (Step, 1932; Edwards & Philp, 2001; Williams, 2008). Williams (2008) reports two nests collected from gardens in south-east London, very small, made of grass clippings, and on the surface in grass-tussocks. His impression is that there is flexibility in selection of nest-sites and this is unlikely to be a limiting factor. Edwards (2008) found nests in scrubby, tussocky grassland close to Salisbury Plain, with characteristics as observed by the above authors. One nest found on Coll was also in tall grass (Edwards, 1999). All available reports of nest-site prospecting females have been of their association with tussocky grassland, often close to hedges or woodland-edge.

Sladen (1912) mentions finding a dead queen alongside the reigning one in a *B. ruderarius* nest – but as Williams (2008) points out, this may indicate competition for established nests, rather than nest-sites. *Thoracobombus* is a sub-genus closely related to *Psithyrus*, and the practice of nest-parasitism is widespread among members of this genus elsewhere than in the UK.

According to Sladen (1912) the cocoons are deep yellow, and the wax dark. He examined 3 nests at an early stage and found the first batch of cocoons in each case to be 8 in number, arranged identically, with two centrally placed, and two lines of three, flanking these. The species (like other 'carders') is a pocket maker, in terms of larval feeding regime. The workers (and queens in the first stage of nest-establishment) feed pollen to groups of larvae by either smearing it on the inner surface of their cell, or by making a 'pocket' on the side of the cell, from which the larvae feed themselves. Sladen (1912) notes a nest found 'at the height of prosperity' in which there were several large such pockets, up to half-an-inch wide and five eighths long, but only one eighth of an inch deep. The pockets were no more than one per cell in number.

Williams (2008) remembers that there were very few workers in the nests he saw. Von Hagen & Aichorn (2003) give 50-100 workers per nest, but this seems a rather high estimate for nests seen in the UK. Løken (1973) cites Lie-Pattersen, in 1899 locating as many as 48 nests in a single farm at Jaeren, Norway. These nests were small, on average containing 25-30 workers.

## 3.3 Reproductive behaviour

Males are reputed to gather round the entrances of nests, waiting to pounce on newly emerging young queens. This seems to be characteristic of the 'carder' bumblebees (sub-genus *Thoracobombus* Dalla Torre) unlike many other species, in which the males often 'patrol' scent-marked routes (Sladen, 1912; Free & Butler, 1959; Edwards, 2008).

## 3.4 Phenology

Most authors give the date of emergence of the queens from hibernation as mid- to late April. One study concurs, recording also the daytime maximum temperature for first emergence (approximately 8°C), significantly later than *B. pratorum, B. terrestris and B. lucorum*, but some days earlier than *B. pascuorum* and *B. lapidarius* (Prys-Jones & Corbet, 1987). According to Sladen (1912) it is the earliest of the 'carder' bumblebees to establish its nest – even earlier than *B. pascuorum*. Alford (1975) also notes that it nests earlier than other species in its sub-genus.

Williams (1989) studied the species at Dungeness from 1974-1984. His pooled data show hibernated queens emerging in mid-April, shortly after those of *B. lucorum* and *B. terrestris*. The first workers were reported from the third week in May, and young queens and males from the second week in July. All three forms continued to be recorded until observation was terminated at the end of August. It is recognised that climatically Dungeness is a 'late' site, and also, the relatively late dates compared e.g. with Essex 1985-1999 might be in part explained by climate change in the intervening period. In Essex, queens are seen as early as the beginning of April in some years and have been observed with pollen loads during the second week of April. However, some may still be seen prospecting for nest sites as late as mid-May. Workers are first seen around the end of April, and males and young queens emerge from the nest from the second week in July onwards. Workers may be seen foraging from the end of April through to as late as the first week in September (Benton, 2000).

Unsurprisingly, Løken (1973) gives the date of first emergence of hibernated queens in Scandinavia as rather later, the end of April, and of first workers on 11th May. However, males are reported from 3rd July, indicating the possibility that the nest cycle is completed more quickly in the more northerly part of its range. The emergence from hibernation of queens in the Suffolk brecks also seems to be rather late, with foraging queens (along with a few probable first-brood workers) seen in late May. Here, too, however, the colony cycle seems short, with males seen in early July (Benton, T. - personal observation).

### 3.5 Parasites, parasitoids and predators

Westrich (1989) mentions the 'cuckoo' bumblebee, *Bombus campestris* as a recorded nest parasite in Germany. *B. campestris* is also mentioned as a nest-parasite of *B. ruderarius* in Switzerland (Amiet, 1996). In the UK another 'carder' bumblebee, *B. pascuorum*, is regarded as the typical host of *B. campestris*, and there are no confirmed reports of *B. ruderarius* as host.

Sladen (1912) states nests of this species are particularly susceptible to infestation by wax moth. Cumber (1949) notes that of 120 surface nests he studied (presumably mostly of 'carder' species) only one was found to be parasitized by wax moth (*A. sociella)*, and this was one of *B. ruderarius* ('…almost completely destroyed at its climax'). Cumber's study, though now some 60 years old, is of considerable interest. He dissected foraging workers of 8 bumblebee species, in addition to worker bees found in the nests of several species, recording the numbers infected by conopid flies. Of only 12 foraging workers of *B. ruderarius* dissected, one was parasitized. One nest studied had only 9 workers, of which 2 were parasitized. However on 8/09/47 he found a *B. ruderarius* nest with 19 conopid pupae (of which 5 later emerged as *Physocephala rufipes*). Those nests of *B. pascuorum, B. humilis* and *B. sylvarum* studied all contained far fewer (from 1-6). Cumber (1949) also includes *B. ruderarius* among the hosts of the very destructive tachinid fly, *Brachycoma devia*, as well as the presumably benign nest associates *Volucella bombylans* and *Fannia* species.

Durrer & Schmid-Hempel (1995) studied parasite loads of bumblebee species in the Jura, Switzerland in 1990 and 1991. In the 2 years of the study *B. ruderarius* was one of the most localised species: present in only 3 sites out of 12 in one year, 6 in the other (our 'common 6' species were recorded each year in 11 or 12 of the sites), and the sample size taken was equal smallest (with *subterraneus*!) both years. They found, as expected, more parasite species per bumblebee species for the locally abundant and widespread bees than in the scarcer and more localised bees. The mean parasite species number per individual host ('parasite load') was also correlated with local abundance and wide distribution. In the case of *B. ruderarius*, parasite diversity varied from 1 to 3 across the 2 years, and parasite load from 0.09 to 0.56. This compared with 4.73/ 4.05 and 0.68/ 0.70 respectively for *B. terrestris/ lucorum*. Their interpretation is that the capacity of the abundant and widespread species to carry a high parasite load is a selective advantage likely to affect local bumblebee assemblages.

# 4. Extent and pattern of decline

The decline in abundance and range of *B. ruderarius* in the UK has been most rapid since the late 1970s/ early 1980s, with a comparatively minor contraction of range prior to that period (Edwards & Philp, 2001). The NBN distribution maps show a distribution for the period 1970 to 1990 significantly reduced compared with that given in the ITE atlas (Anon., 1980) for the date class 1960 to mid-1970s (see Fig.10). The scattered localities in central and northern England (except for a concentration in the far north-east) and inland Wales have disappeared, but the species remains widespread in south-central and south-eastern England. Its continued presence in East Anglia, south Wales, coastal districts of Ireland (especially the west) and Scottish Western Isles is also indicated.

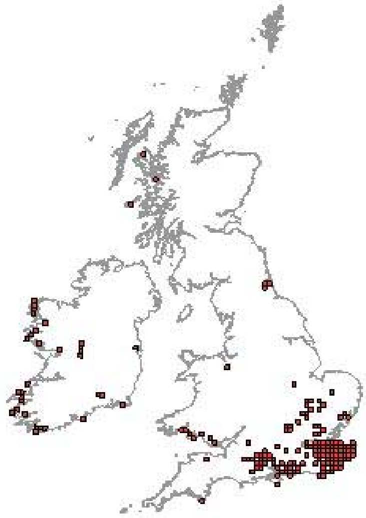

Figure 10: *B. ruderarius* distribution map for period 1970 -1990 (NBN Gateway)

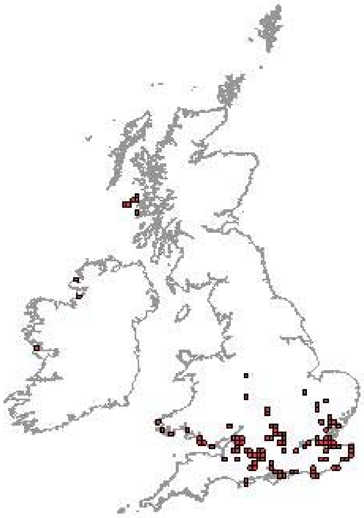

Figure 11: *B. ruderarius* distribution map for period 1991-2008 (NBN Gateway)

However, the date-class 1991-2008 (see Fig.11) shows a very marked change, with much reduced Irish distribution shown, but also a very striking localisation in south and south-central England, where it was formerly widespread. If this latter date-class is broken down, the scale of decline is still clearer, with further apparent losses in southern England, south-Wales and Ireland (see Figs. 12 & 13).

Of course, distribution maps should not be taken at face-value. In part, apparent changes may be related to unevenness of recording coverage, and for this species in particular, there may be problems of field identification (especially from confusion with *B. lapidarius*). However, with increased attention being given to this species following earlier concerns about its conservation status, it seems quite likely that the most recent date-classes do show real trends.

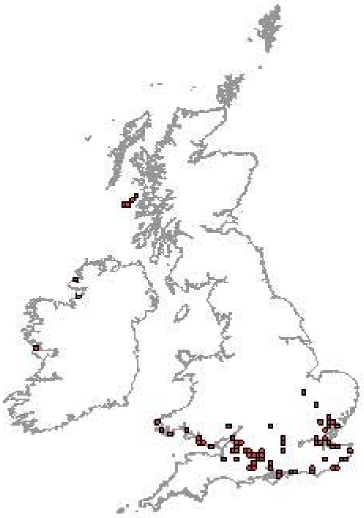

Figure 12: *B. ruderarius* distribution map for period 1991 -1999 (NBN Gateway)

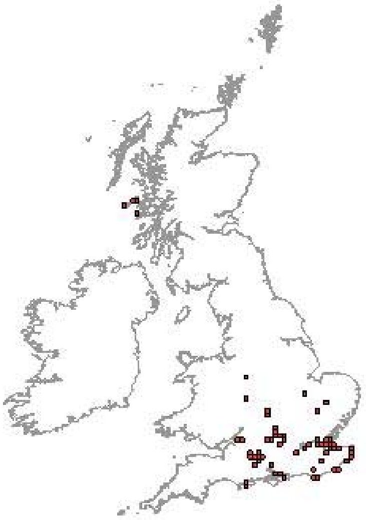

Figure 13: *B. ruderarius* distribution map for period 2000-2008 (NBN Gateway)

# 5. Interpretation

In a series of papers written through the 1980s Williams advanced the view that patterns of bumblebee decline could be interpreted as the result of interaction between three main factors:

1. the foraging efficiency of a species;
2. the width of its climatic range and location of the UK population in relation to that range;
3. changes in the resource-richness of its habitats.

His model predicts that species with narrower climatic ranges or those closer to the edges of their range will be more vulnerable to deterioration in the resource-richness of their habitats and so only survive in patches of resource-rich habitat. In general, their distribution will be increasingly patchy and scattered towards the edge of their climatic range. In Britain, the period of decline in distribution of the widespread local and southern local species coincided with agricultural intensification in lowland Britain. This was likely to have been more significant on the gross scale of Williams's analysis than urbanisation, and took the form, especially in south-eastern and central England, of shifts away from mixed farming to intensive arable cultivation, with loss of hedgerows and other landscape features, and loss or conversion of grassland to silage or 'improved' pasture. The use of agricultural chemicals, all categories of which may be potentially harmful to bumblebees, also increased greatly as an integral part of these changes.

Williams classified the UK species into three groups according to their pattern of distribution: 'mainland ubiquitous' (the common six species – *B. lapidarius, B. lucorum, B. terrestris, B. pascuorum, B. pratorum, B. hortorum* plus *B. ruderarius*), 'widespread local' (including *B. distinguendus, B. soroeensis, B. muscorum* and *B. jonellus*), and 'southern local' (*B. sylvarum, B. humilis, B. ruderatus* and *B. subterraneus*). The species that remained stable belonged to the mainland ubiquitous group, and were all at or close to the centre of their climatic range in the UK. The widespread local species had tended to be closer to the northern limits of their range (or to have narrower ranges) and had retreated northwards in their distribution, whilst the southern local species, being closer to their northern range-limit in the south of the UK had become increasingly localised. This left a large area of central and eastern lowland England in which only the mainland ubiquitous species remained (see Fig.14).

Williams' inclusion of *B. ruderarius* along with the 'big 6' was already somewhat doubtful. Although it had a few outposts in northern and western Scotland, its distribution even then was very skewed to south-eastern England and East Anglia. Williams at one point refers to both *B. lapidarius* and *B .ruderarius* as 'sub-central', noting that while they are near-ubiquitous in south-eastern England they show the expected pattern of becoming increasingly localised further north in their British distribution. In fact, this is much more marked for *B. ruderarius* than it is for *B. lapidarius* (which, since the period for which Williams had evidence, has expanded its presence in Scotland). However, at that point there was rather little to suggest that *B. ruderarius* was about to undergo the decline it appears to have suffered in recent decades.

Of the species that had already undergone marked decline, the 'southern local' species were the ones most clearly comparable in distribution with *B. ruderarius* – with strongly southern or south-eastern distributions, but somewhat more markedly so than *B. ruderarius*. However, the decline of *B. ruderarius* has occurred significantly later, and also shows a somewhat distinctive geographical pattern.

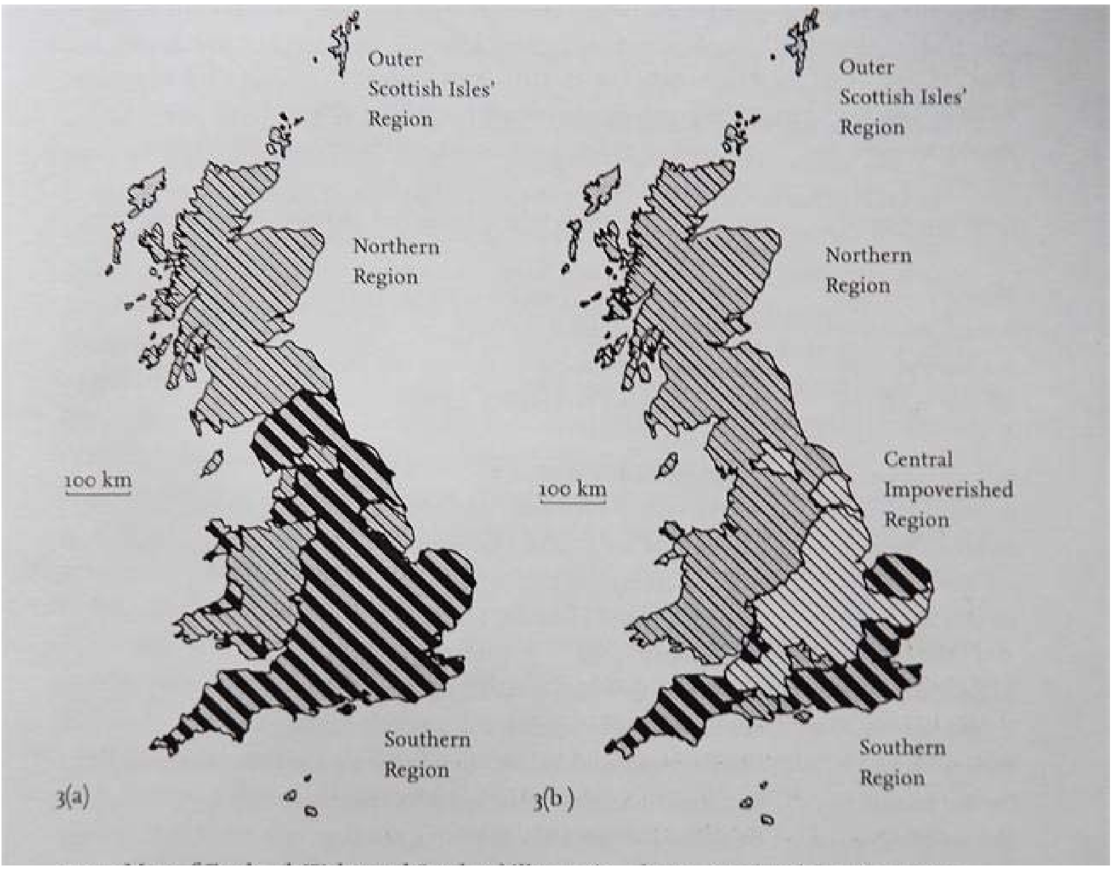

Figure 14: Map of England, wales and Scotland illustrating the geographical distribution of British bumblebee species (a) pre-1960 and (b) 1960 onwards. Dots represent Widespread Local species, narrow lines Mainland Ubiquitous Species and broad stripes Southern Local species (reproduced from Williams, 1982, with permission).

Several authors have proposed other possible explanations for the pattern of bumblebee decline. Most concur on the importance of habitat loss due to agricultural intensification, while doubting the degree of importance attached to climatic range proposed by Williams. Agricultural spraying is mentioned specifically in relation to *B. ruderarius* by von Hagen & Aichorn (2003). Again, factors other than the resource-richness of habitat-patches and energy-efficiency of foraging have been proposed. One feature that Williams reconciles with his own analysis is tongue-length in relation to foraging efficiency. Among the declining species a high proportion are long-tongued species, and if it is supposed that *a.* they forage more efficiently on deep flowers and *b.* agricultural change is particularly affecting the abundance of such flowers, then we have at least a partial explanation of the decline of this group of bees.

Following an assumption of optimal foraging theory as applied to bumblebees, attention has been focussed on foraging efficiency in terms of the single 'currency' of energy conversion. Hence measurement of efficiency of collection of nectar was given priority in research on foraging, with a tendency to neglect the significance of pollen-collection. Rather belated recognition of this led to the hypothesis that species that were quite generalist in their use of nectar sources might be more specialist in their selection of pollen sources and that this might be a factor in the decline of some species (eg. Edwards, 1999; Edwards, 2000; Edwards, 2001; Edwards, 2002; Goulson *et al*., 2005).

Other possible factors included the availability of suitable nest sites, vulnerability to predation or parasitism, and habitat-specialisation. The most persuasive version of this latter idea (Edwards & Williams, 2004) divides bumblebees into two broad groups: those associated with open, flower-rich grassland and those of woodland edge. The latter group were able to use gardens and other urban habitats as resembling woodland edge in significant respects. This division correlates well with the division between local and declining species (of both Williams' 'local' distribution categories) and the surviving ubiquitous species. This division also corresponds well with a division based on phenology. In general the species of open grassland emerge from hibernation and establish their nests later in the spring than do the species of woodland edge and gardens. The latter group tend to have forage sources available early in the year, whereas they tend to be associated with the rather later-flowering Fabaceae of the open grasslands. Finally, more subtle features of competition among the bumblebee species present in a locality might be significant.

The position of *B. ruderarius* is rather anomalous in relation to each of these hypotheses. It is not close to the edge of its climatic range in Britain (and certainly not in the south-east, where its recent decline has been pronounced) nor does it appear to have a narrow climatic range. It does not belong to the long-tongued group, being usually classified as medium-length in this respect, it appears to be a generalist in its foraging preferences, it emerges relatively early from hibernation and does not fit easily into the woodland-edge/ open grassland division in terms of habitat preferences.

As *B. ruderarius* shares many common features of its biology with the other 'carder' bumblebees (sub-genus *Thoracobombus*) it may be illuminating to compare its distribution, status and pattern of decline with theirs. *B. pascuorum* is similarly generalist in its use of forage plants and in the range of habitats it inhabits. It too emerges early from hibernation, is a surface nester and, as a long-tongued species, tends to forage from deep flowers. Both *B. pascuorum* and *B. ruderarius* survive in urban and suburban areas, both nesting in gardens, and using garden plants as forage sources. As would be expected on the habitat specialisation hypothesis, *B. pascuorum* remains ubiquitous and shows no evident signs of decline.

This may, indeed, be a partial explanation of the belated timing of the decline of *B. ruderarius*, but does not appear to explain why an apparent collapse should have occurred in the last 2 to 3 decades – a decline also evidenced in other parts of north/ western Europe. Here, comparison with two other 'carder' species may be relevant. *B. sylvarum* and *B. humilis* are both long-tongued species of open flower-rich grassland, and both quite close to the northern edge of their climatic range. Both species, but especially *B. sylvarum*, suffered huge declines prior to the 1960-1975 period and those losses continued until what may be a small recovery from approximately 2005 in some parts of their range. Both species contracted southwards in range and became more localised in those parts of England and south Wales where they continued to exist. These patterns of decline are consistent with Williams' hypothesised interaction between habitat loss and enhanced vulnerability close to the edge of their climatic range. Williams' expectation that even close to the edge of a species' range, lower foraging efficiency might be compensated by exceptionally rich habitat patches, was borne out in interesting ways by these species. Several of the areas where these species persisted – Salisbury Plain, Castlemartin Ranges and Kenfig/ Margam Moors in South Wales, the Somerset levels – included, as predicted, habitat mosaics with large expanses of unimproved flower-rich grassland. In several examples, subjection to agricultural intensification had been prevented by MoD occupation.

However, a very extensive population persists on both sides of the lower Thames Estuary, using a complex of remnants of old pasture, former mineral extraction sites, sea walls, grazing marshes and former industrial and waste-disposal sites (see figure 14). Parts of this mosaic of habitats do 'mimic' traditionally managed flower-rich grasslands, especially where open areas of nutrient-poor soils have been colonised by plants such as red bartsia, goat's rue, black horehound, black knapweed, narrow-leaved bird's-foot trefoil and clovers. A combination of occasional disturbance, low nutrient levels, and the hot, dry climate may be responsible for the relatively slow pace of succession in many of these habitats, leaving large open areas, interspersed with scrub and hedgerows. In suitable habitat patches in this complex, foraging workers of *B. sylvarum* and *B. humilis* can be abundant – at least as numerous as foragers of the more common species. *B. ruderarius*, too, can occasionally be found in these habitats but it is always in a small numerical minority. However, the same is also true of the other areas where extensive populations of *B. humilis* and *B. sylvarum* still occur, suggesting a degree of difference between habitats favourable to *B. ruderarius* and these relatives.

It seems plausible to suppose that *B. humilis* and *B. sylvarum*, as species of open grasslands, close to the northern edge of their range, have become much more localised as a result of loss of habitat to various processes of agricultural intensification. The main areas where they still survive are extensive, particularly resource-rich, and immune, for a variety of reasons, from agricultural intensification. As species whose colony cycle is completed late in the season, these bees are also extremely vulnerable to early cutting in hay meadows which can eliminate both nests and forage sources. Lack of management or occasional and sporadic disturbance in many of the Thames estuary localities has probably aided the survival of these populations.

*B. ruderarius* differs from these close relatives in several respects. First, while it clearly does survive in extensive open, flower-rich grasslands, as well as the Thames estuary complex, it is rarely abundant there, and it also occurs in a wide range of other habitats – less intensive farmland, coastal dunes and marshes, hedgerows, roadside banks, urban and suburban open spaces, 'wasteground', and gardens. Whilst both *B. humilis* and *B. sylvarum* can be found foraging in gardens, these are generally close to areas of uncultivated ground where their populations are centred, and there is little or no evidence of nesting in gardens. Second, *B. ruderarius* has a quite different phenology. Queens emerge earlier in the spring and establish nests earlier than the other two, and have a relatively short colony cycle. It is less dependent, therefore on either late-flowering grasslands or access to garden flowers late in the season. Both these features (together with its hypothesised generalism as a forager) would lead us to expect it to survive agricultural intensification more successfully than either *B. humilis* or *B. sylvarum*.

Figure 15: Thames Estuary brownfield site at Canvey Island

This still leaves open the questions as to why *B. ruderarius* appears never to have been as common or widespread (even away from its climatic/ geographical limits) as *B. pascuorum*, why *B. ruderarius* appears very rarely to be an abundant species wherever it occurs and why *B. ruderarius* has declined so rapidly over a wide swathe of its range in the UK and western Europe.

In its range of habitats, generalism in its foraging preferences and nesting biology *B. ruderarius* has much in common with its close relative *B. pascuorum*. There is no evidence of a decline in range or abundance for *B. pascuorum* but a steep recent decline in the case of *B. ruderarius*. If we consider that ability to survive in urban and semi-urban habitats, gardens, roadside banks etc has been a factor in the continued abundance of *B. pascuorum* and, possibly, the reason why *B. ruderarius* maintained its status in the south and south-east for longer than *B. sylvarum* or *B. humilis*, then attention should focus on changes in the urban environment. In the UK recent decades have seen very rapid growth in housing (and, to a lesser extent, infra-structural) development. This has been constrained by policy guidelines that prioritise development on brownfield (ie generally urban) rather than 'greenfield' (ie intensive agricultural monocultures) sites. This has had three consequences that may be of significance for the conservation of urban / suburban bumblebee populations, including those of *B. ruderarius*. First, patches of relatively low-intensity management in urban areas are subject to 'infilling' housing development so increasing the fragmentation of suitable nesting and foraging sites. Second, remaining areas of 'green' open space become subject to more intensive forms of 'amenity' management for sports-fields, formal gardens, play areas and the like as the density of human population increases relative to remaining open spaces. Third, untidy, neglected or blighted 'edgelands' that have provided important habitat requirements alongside suburban gardens and open spaces are progressively eliminated or subjected to more formal management routines. Similar processes are noted by Rasmont (2008) who says that urban waste-places in which plants of the Fabaceae and Lamiaceae occurred are 'carefully erased' in Belgium

# 6. Further research

One possibility that could be investigated is that *B. pascuorum* is (so far) better able to maintain the integrity of meta-populations across increasingly hostile and fragmented urban / suburban habitats than is *B. ruderarius*. One route for such an investigation would be to estimate both foraging distances of workers from their nests, and dispersal distances of queens. We already have some measures of the former for *B. pascuorum*, but not for *B. ruderarius*.

Another possibility might relate to the striking differences between the two species in their phenology. *B. pascuorum* queens usually emerge slightly earlier than *B. ruderarius* queens from hibernation (disputed by some authors). Does this give them an advantage in finding nest-sites? Might there be competition between *B. ruderarius* and *B. pascuorum* for nest-sites in their urban habitats? Slight anecdotal evidence for this is the relative frequency with which worn-looking queen *B. ruderarius* may still be seen foraging as late as the end of May (indeed, might there be competition between *B. ruderarius* and the other, scarcer, carders, where they coexist? There appear, for example, to be no confirmed records of *B. pascuorum* on Tiree, where *B. ruderarius* is common, despite being close to the edge of its geographical range).

Another difference in phenology is that *B. pascuorum* nests are often still active into late October in southerly locations, whereas the *B. ruderarius* nest cycle is often complete by mid-July with only few sightings of workers after the end of August. The period during which male and young queens of *B. ruderarius* are on the wing is much shorter than is the case with *B. pascuorum*. The first sexuals of this species may be seen from June through to early November. Given that male *B. ruderarius* will need to locate nests of their own species (presumably other than the 'home' nest) in anticipation of the emergence of possible mates, a high degree of fragmentation of nesting habitat may be a severe limit to reproductive success. It remains unclear, if, and if so, how, the extended seasonal activity-cycle of *B. pascuorum* benefits it.

As to the former rural habitats of *B. ruderarius*, it seems that its less specialised diet (in particular its apparent ability to sustain populations mainly on Lamiaceae in the absence of Fabaceae, Scrophulariaceae or other good pollen sources), and possibly its less specialised nesting habit requirements may have enabled it to survive some aspects of agricultural intensification. Where some hedgerows, banks, unmanaged field-margins, road- and track-sides, cottage gardens, etc. survived, loss of old flower-rich grasslands could be tolerated. Interestingly, though *B. ruderarius* does exist in remaining habitats of this type – as at Kenfig and Salisbury Plain – it is never common even there. It could be that the identification of this species as one of open grasslands is misleading, and that it survives best in the complex habitats formed by later stages of succession from grassland to scrub. Informal and low-intensity management of many urban and urban-fringe open spaces and 'wasteground' would have provided just this sort of habitat complex, as would less-intensively managed mixed farmland. Rather different sets of pressure in each case have led to the loss or fragmentation of such habitats in recent decades. Increasing scarcity and fragmentation of metapopulations of *B. ruderarius* could have been proceeding sub-liminally for some time before they resulted in the contraction of range now evident.

Finally, there is very little evidence concerning predation (including possible nest predation by mammals), parasitism or infestation by microbial pathogens. Apparently some losses of other bumblebee ranges reported from the USA can be attributed to such causes, rather than climatic variables or habitat loss (Williams, 2008). This is, of course, a real possibility as a factor in the decline of *B. ruderarius*, but there is little if any recent relevant evidence.

# 7. Conservation measures

There appears to be some evidence that habitat improvement measures on arable land by re-seeding to flower rich grassland initially benefit this species, if a local population is already present (Else in Edwards, 2001 and Edwards, 2002). It seems unlikely that of itself provision of conservation strips comprising bumblebee forage plants on otherwise intensively farmed land will benefit this species (as it appears to have done in the case of *B. ruderatus*). However, experimental provision of suitable foraging habitat in conjunction with other changes in land management might well prove to be of benefit, so long as there is a local population available to colonise it. Close study of the foraging and nesting behaviour and habitat of *B. ruderarius* is urgently needed. This, of course, will require location of a study-site where regular sighting of *B. ruderarius* can be relied upon.

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