

**Effects of habitat composition and landscape structure on
worker foraging distances of five bumblebee species**

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1 **Effects of habitat composition and landscape structure on worker foraging distances of five**
2 **bumblebee species**

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23 **Summary**

- 24 1. Bumblebees (*Bombus* spp.) are important pollinators of both crops and wild flowers. Their
25 contribution to this essential ecosystem service has been threatened over recent decades by
26 changes in land use, which have led to dramatic declines in their populations. In order to design
27 effective conservation measures it is important to understand the effects of variation in
28 landscape composition and structure on the foraging activities of bumblebees. However, these
29 issues remain poorly understood.
- 30 2. We used field surveys, molecular genetics and fine resolution remote sensing to estimate the
31 locations of wild bumblebee nests from the locations of related workers across a 20 km²
32 agricultural landscape in southern England, for five species, including the rare *B. ruderatus*. We
33 compared worker foraging distances between species and examined how variation in landscape
34 composition and structure affected patterns of foraging.
- 35 3. Mean worker foraging distances differed significantly between species. *Bombus terrestris*, *B.*
36 *lapidarius* and *B. ruderatus* exhibited significantly greater mean foraging distances (around 500
37 m) than *B. hortorum* and *B. pascuorum* (around 300 m).
- 38 4. There was wide variation in worker foraging distances between colonies of the same species.
39 This variation was strongly influenced by the amount and spatial configuration of available
40 foraging habitats in the local landscape. Shorter foraging distances were found for colonies
41 where the local landscape had a high coverage and low fragmentation of semi-natural
42 vegetation including managed agri-environmental field margins. Floral cover of preferred forage
43 plants had the strongest effects on worker foraging distance.
- 44 5. *Synthesis and applications.* The amount and spatial configuration of floral resources are
45 important in determining the foraging distances of worker bumblebees. This may underlie one
46 of the mechanisms contributing to the decline of some bumblebee species with land use
47 change, as in resource-poor landscapes workers must travel further to collect sufficient

48 resources, incurring higher energetic costs. The strength of the relationships found between
49 foraging habitat and worker foraging distance also suggests that there is potential for
50 improvements to be made in the design and implementation of agri-environment options
51 aimed at providing foraging habitat for bumblebees.

52 Keywords: Spatial ecology, *Bombus*, wild colonies, pollination, foraging range, landscape scale, Agri-
53 environment

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56 **Introduction**

57 Bumblebees are important pollinators of wild plants (Holzschuh *et al.* 2011; Kovács-Hostyánszki *et*
58 *al.* 2013) and a range of crops (Garratt *et al.* 2014). They therefore provide an essential ecosystem
59 service, affecting the stability of natural ecosystems as well as agricultural productivity. Many
60 bumblebee species worldwide have undergone declines, driven by a range of factors including
61 habitat loss and fragmentation following agricultural intensification (Williams & Osborne 2009). As a
62 result there is great interest in the likely impacts of ongoing modifications to the landscape on
63 ecosystem service delivery by bumblebees, and in methods by which landscapes might be enhanced
64 in terms of suitability for bumblebee populations. Such methods include the many agri-environment
65 schemes whose aims include providing foraging resources for pollinating insects (Carvell *et al.* 2006;
66 Carvell *et al.* 2007).

67 As worker bumblebees are central place foragers, the spatial and temporal distribution of resources
68 surrounding the colony is important in determining the energetic returns of foraging trips and
69 ultimately the viability of a colony (Dukas & Edelman-Keshet 1998). Many models of pollinator
70 foraging and pollination services rely on accurate parameterisation of foraging distance and resource
71 value of different habitats (Cresswell, Osborne & Goulson 2000; Lonsdorf *et al.* 2009; Raine, Rossmo
72 & Le Comber 2009). Indeed, if land management for bumblebees is to be successful (and cost
73 effective), it is important to have accurate information on how far workers travel to forage and the
74 extent of variation within and between species. However, this information is currently limited for
75 wild colonies of most bumblebee species, and there is a corresponding lack of knowledge on how
76 landscape composition and structure affect foraging patterns.

77 Wild colonies of many species of bumblebee are subterranean or concealed in dense vegetation,
78 making them difficult to find. Therefore studies of worker foraging distance have tended to rely

79 upon observations of workers from small numbers of wild or experimentally reared colonies
80 (Walther-Hellwig & Frankl 2000; Westphal, Steffan-Dewenter & Tschardt 2006b; Osborne *et al.*
81 2008), inferences from worker density and landscape composition (Westphal, Steffan-Dewenter &
82 Tschardt 2006a; Suzuki, Kawaguchi & Toquenaga 2007) or genetic analyses of bumblebees
83 captured at foraging sites (Chapman, Wang & Bourke 2003; Darvill, Knight & Goulson 2004; Knight *et*
84 *al.* 2005; Charman *et al.* 2010; Dreier *et al.* 2014b). The first two approaches exhibit various
85 limitations: studies are too labour-intensive to apply to large samples or must make simplifying
86 assumptions about resource distribution and constancy of foraging ranges. In contrast, genetic
87 analyses permit inferences regarding bumblebee spatial ecology based on large numbers of wild
88 colonies. Such studies typically involve sampling worker bees and reconstructing colony
89 memberships on the basis of individual multilocus genotypes to obtain numbers or densities of
90 colonies (Herrmann *et al.* 2007; Knight *et al.* 2009; Goulson *et al.* 2010). Recently, these methods
91 have also been used to estimate the foraging distances of individual colonies (Carvell *et al.* 2012; Jha
92 & Kremen 2013). However, so far such studies have used data from workers sampled at discrete
93 sites (e.g. spatially separated forage patches or transects), constraining the range of foraging
94 distances and spatial patterns that they are able to detect.

95 In this study, we used genetic analyses to estimate worker foraging distances for five social
96 bumblebee (*Bombus*) species (including *B. ruderatus* Fabricius which is rare in the UK and in decline
97 throughout Europe) and combined these with data on habitat and floral resources to answer the
98 following questions. Firstly, how does the distance that workers travel from the colony to forage
99 vary between species sampled across a common landscape? Secondly, do the distances travelled by
100 workers vary between colonies within species depending on their location in the landscape? Thirdly,
101 how do habitat composition and landscape structure affect worker foraging distance?

102 We sampled workers across the entirety of a landscape that varied in habitat composition and had
103 been mapped at a fine spatial resolution. This is the first time that this approach has been applied at

104 such a fine spatial scale and to both common and declining species within a shared landscape. Our
105 methods have the advantages of increasing the likelihood of detecting sister workers at multiple
106 sites and of sampling a high proportion of colonies in the landscape (Dreier *et al.* 2014b). We found
107 significant effects of both habitat composition and landscape structure on the estimated foraging
108 distances of workers from different colonies, and discuss the implications of our findings for
109 effective management for bumblebee conservation within agricultural landscapes.

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112 **Methods**

113 STUDY LANDSCAPE AND STUDY SPECIES

114 The study was conducted over a 20 km² area of farmland centred on the Hillesden Estate,
115 Buckinghamshire, UK (51.95 N, 01.00 W; Fig. S1). The landscape is typical of southern lowland
116 England, being dominated by arable fields of autumn-sown wheat *Triticum aestivum* L., oilseed rape
117 *Brassica napus* L. and field beans *Vicia faba* L., interspersed with fields of permanent pasture (mostly
118 ryegrass *Lolium perenne* L. and white clover *Trifolium repens* L.) and scattered small woods and
119 copses. Most fields are bordered by low (<2 m), shrub hedgerows with scattered, mature trees. The
120 landscape also contains several small villages, giving some cover of gardens and associated suburban
121 vegetation. The Hillesden Estate itself forms around 10 km² of the study landscape. This estate has
122 been managed since 2005 under a range of agri-environment options typical of the UK's entry level
123 stewardship (ELS) agri-environment scheme. These include field margins and field corners sown
124 with grass, perennial wildflower and annual bird food seed mixes aimed at promoting a range of
125 farmland biodiversity target taxa including pollinating insects (see Redhead *et al.* (2013) and
126 Broughton *et al.* (2014) for further details).

127 Of the five study species, four are common and widespread across much of the UK (*B. terrestris* L.,
128 *B. lapidarius* L., *B. pascuorum* Scopoli, *B. hortorum* L.) while one (*B. ruderatus*) has suffered
129 significant declines in recent decades and is a conservation priority species listed under Section 41 of
130 the UK Natural Environment and Rural Communities Act 2006 (NERC 2006). The five species vary in
131 their forage plant choice and nesting behaviours. *Bombus terrestris* and *B. lapidarius* typically have
132 large colonies and short-tongued workers that visit a wide range of flowers, whereas *B. pascuorum*
133 and *B. hortorum* tend to live in smaller colonies and have longer-tongued workers that specialize in
134 foraging at flowers with long corolla tubes (Benton 2006). *B. ruderatus* is ecologically similar to *B.*
135 *hortorum*, these being the longest-tongued UK *Bombus* species.

136 BUMBLEBEE SAMPLING AND GENETIC ANALYSIS

137 Workers of all five study species were sampled between 20th June and 5th August 2011, using
138 gridded survey maps to ensure full coverage of the entire study landscape (see Supplementary
139 material Fig. S1. and Dreier *et al.* (2014b) for full details). All encountered workers of the target
140 species were caught, their locations recorded using a handheld GPS (Garmin Etrex 10, accurate to 3
141 m) and foraging behaviours noted. The identity of the visited forage plants was also recorded. The
142 tarsal tip was non-lethally removed from the right mid-leg of each bee (Holehouse, Hammond &
143 Bourke 2003), and preserved in 100% ethanol until DNA extraction. DNA was isolated from each
144 tarsal sample using the standard HotSHOT protocol (Truett *et al.* 2000). Field identification to species
145 was subsequently confirmed with PCR-based molecular identification tools (Dreier *et al.* 2014a;
146 Dreier *et al.* 2014b) for the species pairs *B. hortorum*/*B. ruderatus* and *B. terrestris*/*B. lucorum* L., in
147 which the workers are difficult to separate using morphological characters alone. Individuals were
148 then genotyped at 10-14 microsatellite loci (Dreier *et al.* 2014a). Sister relationships among workers
149 were estimated from individual marker genotypes using the maximum likelihood sibship
150 reconstruction method in COLONY version 2.0 (Wang 2004). For full details of the genetic analysis,
151 see Dreier *et al.* (2014a, 2014b)

152 COLLECTING HABITAT DATA

153 Survey maps of habitat data were based on a land use/land cover (LULC) map derived from two
154 airborne remote sensed sources - Light Detection and Ranging (LiDAR) and hyperspectral imaging.
155 These remote sensed data were acquired by the Natural Environment Research Council Airborne
156 Research and Survey Facility on 28th August 2007. Supervised classification of the hyperspectral
157 dataset, combined with a digital canopy height model derived from LiDAR, produced a high
158 resolution (0.5 x 0.5m pixels) LULC map. For further details on the collection and processing of the
159 LiDAR and hyperspectral data, see Redhead *et al.* (2013). For the current study, the LULC map was
160 simplified to nine classes - arable, short grass, mixed low vegetation, garden and urban vegetation,

161 woody vegetation, ELS field margin, road and building, water, bare soil (see Figure 1 and
162 supplementary material, Figure S1) - and updated manually to reflect changes in ELS management.
163 The LULC map was used to systematically survey the study landscape in terms of its value for
164 bumblebees. Every mapped LULC polygon representing a discrete habitat parcel (i.e. an area of
165 contiguous land use clearly visible in the field) was surveyed during July and August 2011, to
166 estimate the percentage flower cover (i.e. vegetative cover multiplied by proportion in flower) of
167 target plant species, families or groups (given in Supporting Information, Table S1). Any changes in
168 the extent of parcels identified in the field were manually added to the LULC map. In total, 18.7 km²
169 of the study landscape were surveyed in this way. For the remaining 6.5% of the study area that was
170 not surveyed (because of access restrictions, mostly on pasture fields and suburban areas on the
171 edge of the study area), floral data were estimated by taking the mean cover of values from parcels
172 of the same LULC class within 500 metres of the focal parcel. Handling of the LULC map and survey
173 data, and estimation of colony locations (see below), was performed in ArcMAP v10.0 (© ESRI,
174 Redlands, CA, USA).

175 ESTIMATING COLONY LOCATIONS, FORAGING DISTANCES AND RELATIONSHIPS WITH LANDSCAPE VARIABLES

176 Locations were estimated for all colonies from which two or more sister workers had been inferred
177 in the sample. Colonies from which only a single worker was inferred ('singletons') were excluded
178 from further analyses as they cannot yield a meaningful estimate of colony location (Carvell *et al.*
179 2012). Estimated colony locations were derived using a mean centre approach. This took the mean
180 Easting and Northing of worker locations from each sibship and plotted the resultant coordinates
181 (Fig. 1). This 'mean centre' approach had several advantages over other methods tested in
182 preliminary analyses (Carvell *et al.* 2012; Dreier *et al.* 2014b). These locations were then 'snapped'
183 (i.e. moved to coincide exactly with the coordinates of another feature) to the nearest LULC class
184 that might have formed suitable nesting habitat for bumblebees (i.e. all classes except arable fields,

185 roads, buildings and water). Most locations did not require snapping, and, of those that did, 80%
186 were moved less than 50 m.

187 The straight-line distance of each worker to its estimated colony location was calculated. The mean
188 of these distances for all workers in a colony was then calculated to give a 'colony-specific foraging
189 distance'. To estimate the resource quality of the landscape surrounding each colony, a buffer with
190 a radius equal to its colony-specific foraging distance was created around the colony location (Figure
191 1). The proportion of each LULC class (mixed low vegetation and ELS margins being combined to a
192 single 'mixed vegetation' class, i.e. to include non-woody, non-crop, forbs or forb-grass mixtures)
193 and the floral cover of plant groups within this buffer were then determined. Floral cover of
194 surveyed plant groups was further grouped in terms of the plants' relative value as forage resources
195 for bumblebees. These groupings were 'non-crop', 'visited' (visited by foraging workers during
196 sampling) and 'preferred' (the five plant groups with the highest mean number of observed worker
197 visits to species within the group, as listed in Supporting Information, Table S1). Three metrics of
198 landscape structure were also calculated within the buffer area, chosen on the basis of having been
199 demonstrated to provide ecologically informative measures of the spatial configuration of habitats
200 (Riitters *et al.* 1995; Moser *et al.* 2002) or to influence the foraging distances of bumblebees
201 (Cranmer, McCollin & Ollerton 2012):

- 202 i. Mean patch edge:area ratio for patches of mixed vegetation; a measure of the
203 fragmentation of resource patches surrounding each colony, incorporating patch size.
- 204 ii. Mean shape index for patches of mixed vegetation, calculated as patch perimeter divided by
205 the square root of patch area, multiplied by 0.25; a measure of the average complexity of
206 patch shapes (equalling one for perfectly square patches, decreasing without limit as
207 patches become more irregular), independent of patch area.

208 iii. Hedgerow proximity index, calculated by summing the distance to the nearest three
209 hedgerow intersections; an index of the amount and complexity of hedgerow in the local
210 landscape.

211 STATISTICAL ANALYSIS

212 The relationship between each habitat variable and log (base 10) transformed colony-specific
213 foraging distance was analysed for each species by independent general linear models (GLM)
214 performed in R (R Core Team 2013). Colonies with less than 95% coverage of habitat data within the
215 buffer were excluded from these analyses (n= 21). Colonies with a mean colony-specific foraging
216 distance of less than 20 m were also excluded (n = 25). The latter were excluded because such
217 colonies were likely to have resulted from sampling related workers in a single resource patch. We
218 then examined R^2 and AIC values from each GLM to identify the best fitting models.

219

220

221 **Results**

222 A total of 2577 workers were sampled and genotyped from the five target species (sample sizes
223 given in Table 1). The total estimated number of colonies within the landscape varied between
224 species (Table 1), but not in direct proportion to the number of individual workers sampled, with
225 some species having higher proportions of singletons (e.g. *B. hortorum* and *B. terrestris*).

226 Worker foraging distances differed significantly between species (Table 1, One-way ANOVA, $F_{4, 1551} =$
227 26.42, $p < 0.01$). Species mean foraging distances formed two groups (Tukey post-hoc tests,
228 Supporting Information, Table S2) - with shorter distances of around 300 m for *B. pascuorum* and
229 *B. hortorum* and significantly longer distances of around 500 m for *B. terrestris*, *B. lapidarius* and
230 *B. ruderatus*. Maximum foraging distances were considerably greater, with an individual worker of *B.*
231 *terrestris* reaching 2878 m from its estimated colony location (see Table 1 for other species maxima).
232 There was no consistent effect of size of sibship on estimated foraging distance, for any species.

233 Colony-specific foraging distances varied widely between colonies of the same species. A range of habitat
234 variables showed significant relationships with colony-specific foraging distances across species (Table 2).
235 Overall there was a strong, significant negative effect of cover of mixed vegetation, such that increasing cover
236 decreased the colony-specific foraging distances of all species (Fig. 2). This relationship was markedly weaker
237 for *B. terrestris*. Cover of arable land showed the reverse relationship (Fig. 2), such that greater arable cover
238 resulted in greater colony-specific foraging distances. This relationship was strongest for *B. terrestris* and *B.*
239 *lapidarius*.

240 Significant effects of floral cover on colony-specific foraging distances were found only for non-crop
241 vegetation. A significant, negative relationship between colony-specific foraging distance and non-crop floral
242 cover surrounding the colony was observed for all species, with highest model fit for longer-tongued species
243 (*B. pascuorum*, *B. hortorum* and *B. ruderatus*). Limiting the floral cover data to worker-visited plant groups
244 made little difference to model fit. However, further refinement of to worker-preferred plant groups improved
245 the explanatory power of the models (Table 2), especially for the two long-tongued species *B. hortorum* and *B.*

246 *ruderatus*. The decline in colony-specific foraging distance with increased worker-preferred floral cover was
247 also notably steeper for these two species (fig. 3).

248 Among the landscape structure metrics, there was a significant positive relationship between colony-specific
249 foraging distance and mean edge area ratio for all species (Table 2). For *B. terrestris*, *B. lapidarius* and *B.*
250 *ruderatus*, mean edge area ratio was a better predictor of colony-specific foraging distance than proportion of
251 mixed vegetation. For *B. hortorum* and *B. pascuorum*, the opposite was true, with mean edge area ratio of
252 secondary importance compared to proportion of mixed vegetation. In contrast, shape index only had a
253 significant effect in *B. hortorum* and *B. pascuorum*, and in neither case did it improve model fit above total
254 cover of mixed vegetation. The hedgerow proximity index showed low model support for all species (Table 2).

255

256

257 **Discussion**

258 In this study we used genetic analyses to determine colony membership for worker bumblebees of
259 five species sampled across an agricultural landscape and thereby estimate colony locations and
260 foraging distances at the level of individual workers. We found significant differences in worker
261 foraging distances between the five study species, which could be divided into 'long' (*B. lapidarius*,
262 *B. terrestris* and *B. ruderatus*) and 'short' (*B. hortorum*, *B. pascuorum*) range foragers. We also
263 showed that the colony-specific foraging distance varied widely within each species depending on
264 the location of colonies within the landscape with respect to the availability and configuration of
265 floral resources. This confirms the potential for bumblebees to show foraging plasticity in response
266 to changes in resource availability (Jha & Kremen 2013), but suggests that differences between
267 species and the scale of land-use changes could be critical in designing management practices to
268 conserve bee populations and enhance pollination services.

269 VARIATION IN WORKER FORAGING DISTANCES BETWEEN SPECIES

270 Our estimates of mean and maximum foraging distance for each species (Table 1) fell within the
271 range of previous estimates for *B. terrestris*, *B. lapidarius* and *B. pascuorum*. Despite variation in
272 both these estimates and our colony-specific foraging distances, our results confirm that *B. terrestris*
273 workers may forage several kilometres from the colony (Walther-Hellwig & Frankl 2000; Knight *et al.*
274 2005; Westphal, Steffan-Dewenter & Tschardt 2006a; Osborne *et al.* 2008) and that *B. pascuorum*
275 generally travels shorter distances (Darvill, Knight & Goulson 2004; Knight *et al.* 2005), although
276 occasional individuals can still be found almost two kilometres from the colony (Chapman, Wang &
277 Bourke 2003; Carvell *et al.* 2012). While some studies have suggested that *B. lapidarius* has a similar
278 mean foraging range to *B. pascuorum* (Knight *et al.* 2005; Carvell *et al.* 2012), our results indicate
279 that *B. lapidarius* is more similar in its foraging range to *B. terrestris* (Walther-Hellwig & Frankl 2000;

280 Westphal, Steffan-Dewenter & Tschardtke 2006a), as might be predicted from the similar ecology
281 and population status of the two species.

282 No previously published foraging distances are available for *B. hortorum* or *B. ruderatus*. Both are
283 long-tongued species, with a high level of specialisation on long-corolla flowers such as red clover,
284 *Trifolium pratense* L. (Carvell *et al.* 2006), lending them particular ecological importance as
285 pollinators (Garratt *et al.* 2014). However, the two species have shown contrasting population
286 trends, with *B. hortorum* remaining widespread throughout Europe (Goulson *et al.* 2005) and
287 *B. ruderatus* showing significant contractions in its native range. Our results showed *B. hortorum* to
288 have the shortest mean and maximum worker foraging distances of the five species, whereas the
289 values for *B. ruderatus* were relatively high. This is counter to the expectation that species with the
290 shortest foraging ranges should be most at risk from lack of forage in the local landscape, and thus
291 most threatened by changes in land use. It is therefore unlikely that the typical foraging distance
292 alone determines the species-level response to landscape changes.

293 RELATIONSHIPS BETWEEN HABITAT COMPOSITION AND COLONY-SPECIFIC FORAGING DISTANCES

294 The amount of floral resources provided by non-crop vegetation, whether measured directly or by
295 proxy as cover of the mixed vegetation landcover class, always showed a significant negative
296 relationship with foraging distance, such that colonies in areas of the landscape with least floral
297 resources had on average more distantly-foraging workers (Table 2). Longer foraging distances may
298 be either beneficial or injurious at the colony level, since workers face a trade-off between the
299 increased costs of foraging and potential energetic gains (Schmid-Hempel & Schmid-Hempel 1998;
300 Cresswell, Osborne & Goulson 2000). Although relationships between habitat and foraging distance
301 should be interpreted with caution, due to potential influences from variables not measurable by the
302 methods of this study (e.g. differing mean body size, colony size, population density, intensity of
303 competition), our results suggest that contrasting situations may occur in different species.

304 Widespread species with longer foraging distances, such as *B. terrestris* and *B. lapidarius*, may be

305 more flexible in their ability to compensate for a resource-poor local landscape by increasing search
306 effort to find more distant patches of high quality forage (Walther-Hellwig & Frankl 2000; Westphal,
307 Steffan-Dewenter & Tschardt 2006a; Osborne *et al.* 2008). These two species have been observed
308 to dominate the bumblebee communities of modern arable land (Bommarco *et al.* 2011). As short-
309 tongued generalists, such species also have the widest range of potential food sources, and so are
310 most likely to find viable resources by increasing foraging distance. This is supported in our study by
311 the comparatively weak relationships with habitat displayed by *B. terrestris* and *B. lapidarius*. In
312 contrast, *B. ruderatus* was the only species to show a longer mean foraging distance and yet retain
313 strong relationships between colony-specific foraging distance and floral cover, especially with the
314 worker preferred floral cover, which included red clover. These findings are a likely consequence of
315 its specialised flower choices, such that workers from nests in resource-poor parts of the landscape
316 must travel long distances to reach suitable forage patches. They may not, however, be able to
317 reach a point where the proportional cover of resources offsets the costs of increased travel. Similar
318 situations may hold for other rare or declining species such as *B. distinguendus* Morawitz, the only
319 other rare UK bumblebee species for which foraging distance has been directly studied. This species
320 also has relatively long foraging distances, and a similar level of specialisation on floral resources
321 which are increasingly less common under agricultural intensification (Charman *et al.* 2010).

322 Neither *B. pascuorum* nor *B. hortorum* are showing the declines that might be expected given their
323 comparatively short average foraging distances and strong relationships between foraging distance
324 and local habitat, although there is evidence that their prevalence in the bumblebee community has
325 declined in modern arable landscapes (Bommarco *et al.* 2011). *Bombus pascuorum* has a medium
326 tongue-length and has been associated with a wide range of forage plants (Dramstad & Fry 1995),
327 including flowering crops (Herrmann *et al.* 2007; Garratt *et al.* 2014). This lack of specialisation, seen
328 in our results by the low increase in model fit between non-crop and worker preferred floral cover,
329 may allow it to maximise the value of the local area by intensive use of all available resources, as
330 suggested for the related *B. muscorum* L. by Walther-Hellwig and Frankl (2000). The widespread

331 status of *B. hortorum* despite its similarity to the declining *B. ruderatus* has been a continuing
332 enigma, with suggested explanations including differences between the species in their proximity to
333 the edges of their global distributions (Goulson *et al.* 2005) and, as recent evidence from the current
334 study landscape suggests, lower colony densities and levels of genetic diversity in *B. ruderatus*
335 (Dreier *et al.* 2014b). Our results add to these findings by suggesting that *B. ruderatus* uses the
336 landscape at a different spatial scale, more similar to that of *B. lapidarius* and *B. terrestris*, despite an
337 apparent preference for a restricted subset of plant groups where they occur.

338 For all species, total floral cover including cover of flowering crops did not show a significant effect
339 on colony-specific foraging distance. A similar result was found for *B. vosnesenskii* (Radoszkowski) in
340 the USA by Jha and Kremen (2013), with no apparent effect of total floral cover, although there are
341 considerable differences in spatial scale and sampling approach between the study of Jha and
342 Kremen (2013) and the current study. The most abundant flowering crop in our landscape (and in
343 the UK), oilseed rape, has been implicated in affecting bumblebee colony size, local worker
344 abundance and worker foraging patterns, but these effects can be short-lived, due to its
345 comparatively short flowering period (Westphal, Steffan-Dewenter & Tschardt 2003; Westphal,
346 Steffan-Dewenter & Tschardt 2009; Kovács-Hostyánszki *et al.* 2013; Persson & Smith 2013). In the
347 present study, surveys were conducted well after the peak flowering period of oilseed rape so that
348 even later-flowering fields are likely to have already declined in value, and indeed no workers were
349 observed foraging on oilseed rape in our study. Such a lack of response to mass-flowering crops
350 emphasizes the importance of longer-flowering semi-natural resources for sustaining the full colony-
351 cycle of bumblebees.

352 RELATIONSHIPS BETWEEN LANDSCAPE STRUCTURE AND COLONY-SPECIFIC FORAGING DISTANCES

353 The spatial arrangement of resources is well established as a potential driver of pollinator
354 abundance and foraging patterns (Rundlof, Nilsson & Smith 2008; Cranmer, McCollin & Ollerton
355 2012), and, at larger scales, habitat fragmentation is frequently cited as a major driver of

356 biodiversity loss (Krauss *et al.* 2010). At the scale of the current study, it was evident that landscape
357 structure was important to varying degrees for the different species of bumblebee.

358 In agricultural landscapes dominated by large open spaces, linear features, like hedgerows, may
359 provide important flyways for pollinators that facilitate movement between forage patches
360 (Cranmer, McCollin and Ollerton (2012) . Our study found only weakly supported relationships
361 between the abundance and proximity of hedgerows in the local landscape and worker foraging
362 distances. This does not mean that hedgerows are not important to worker movements but rather
363 that in our landscape hedgerows did not promote a significant increase in the mean distance
364 travelled.

365 Species with longer foraging distances responded more strongly to edge area ratio than to total
366 cover of mixed vegetation. Edge area ratio decreases with increasing patch area, such that
367 landscapes with a low edge area ratio are likely to be composed of large, compact foraging resource
368 patches, while those with a high edge area ratio will reflect greater fragmentation.

369 *Bombus ruderatus* showed the strongest relationship with this variable, corroborating previous
370 suggestions that *B. ruderatus* requires not only the presence of long corolla flowers but large,
371 continuous tracts of habitat containing these species (Goulson *et al.* 2005).

372 Over longer foraging distances, travel between patches becomes more feasible, as does covering an
373 elongated or irregular patch, so it might be expected that total area and fragmentation are more
374 important than the shape of patches for species foraging over greater distances. Indeed,
375 *B. terrestris*, *B. lapidarius* and *B. ruderatus* did not show any significant relationship with patch shape
376 index. Although *B. hortorum* and *B. pascuorum* did show a significant relationship, patch shape
377 index added little to the amount of variation explained by total mixed vegetation cover. Thus a
378 larger total area of floral resource, in large patches, spaced within the mean foraging range of the
379 species, remains the most beneficial situation for all five species. This is in some respects supportive

380 of current UK agri-environmental practice as many options targeted at pollinators are implemented
381 as field margins and are thus linear in nature, helping to decrease distance between patches.

382 IMPLICATIONS FOR DESIGN AND IMPLEMENTATION OF LAND MANAGEMENT FOR BUMBLEBEE CONSERVATION

383 Overall our study suggests that even within a relatively small landscape area, bumblebee worker
384 foraging distances vary according to resource availability. Several studies have asserted that
385 common bumblebees may form useful proxies for rare, and thus more difficult to study, species by
386 virtue of shared ecological attributes such as nesting ecology, tongue-length or life-cycle (Walther-
387 Hellwig and Frankl 2000, Jha and Kremen 2013). By sampling both common and rare species within
388 a shared landscape, our study shows that even ecologically and morphologically similar species can
389 respond to landscape composition and structure in different ways, and that this may provide insight
390 into the causes of their different trends at a population level (Osborne et al. 2008a).

391 Our results suggest that provision of floral resources under agri-environment schemes, for example
392 by sowing of targeted wildflower mixtures (Carvell et al., 2007), is likely to reduce net energy
393 expenditure by reducing the distance workers are required to travel in order to forage, for many
394 bumblebee species. These effects are likely to be most pronounced where resources are sited in
395 such a way as to increase connectivity at a scale relevant to the foraging range of most colonies. Our
396 estimates suggest that, in the study landscape, 5 - 10% floral cover of non-crop, semi-natural
397 vegetation or 1 - 3% floral cover of preferred forage species should allow workers of the studied
398 bumblebee species to forage at or below their species mean distance from the colony. Reducing
399 energy expenditure is likely to enhance the survival of colonies and contribute to promoting
400 bumblebee population stability and growth. However, further work on the impact of the landscape
401 on colony survival and dispersal over time would be valuable in quantifying the importance of forage
402 at different times of year, and the requirements for nesting and overwintering sites, all of which are
403 also potential targets for conservation management.

404

405

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418

419 **Data Accessibility**

420 Microsatellite genotype data for five species of bumblebee across an agricultural landscape in

421 Buckinghamshire, UK. NERC Environmental Information Data Centre: DOI: 10.5285/6a408415-0575-

422 49c6-af69-b568e343266d

423 Location data of worker bumblebees across an agricultural landscape in Buckinghamshire, UK. NERC

424 Environmental Information Data Centre (EIDC): DOI: 10.5285/a60f52b8-0f9f-44f6-aca4-

425 861cb461a0eb

426 Map of land-use/land-cover and floral cover across an arable landscape in Buckinghamshire, UK.

427 NERC Environmental Information Data Centre (EIDC): DOI: 10.5285/0667cf06-f2c3-45c1-a80a-

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551

552 **Table 1.** Sample sizes (N) and descriptive statistics for worker foraging distances, for each of the five
 553 *Bombus* species. Sample sizes are given with and without 'singletons' (colonies from which only a
 554 single worker was sampled).

Species	Worker foraging distance (m)					Colonies	
	N all workers	N non-singletons	Mean	SE	Max	N all colonies	N non-singleton colonies
<i>B. terrestris</i>	382	187	551.40	39.83	2878.00	264	69
<i>B. lapidarius</i>	1171	774	536.39	16.02	2059.00	668	271
<i>B. pascuorum</i>	548	311	336.86	19.92	1808.00	360	123
<i>B. hortorum</i>	262	117	272.98	20.15	810.00	193	48
<i>B. ruderatus</i>	214	168	501.62	33.71	2350.00	88	42

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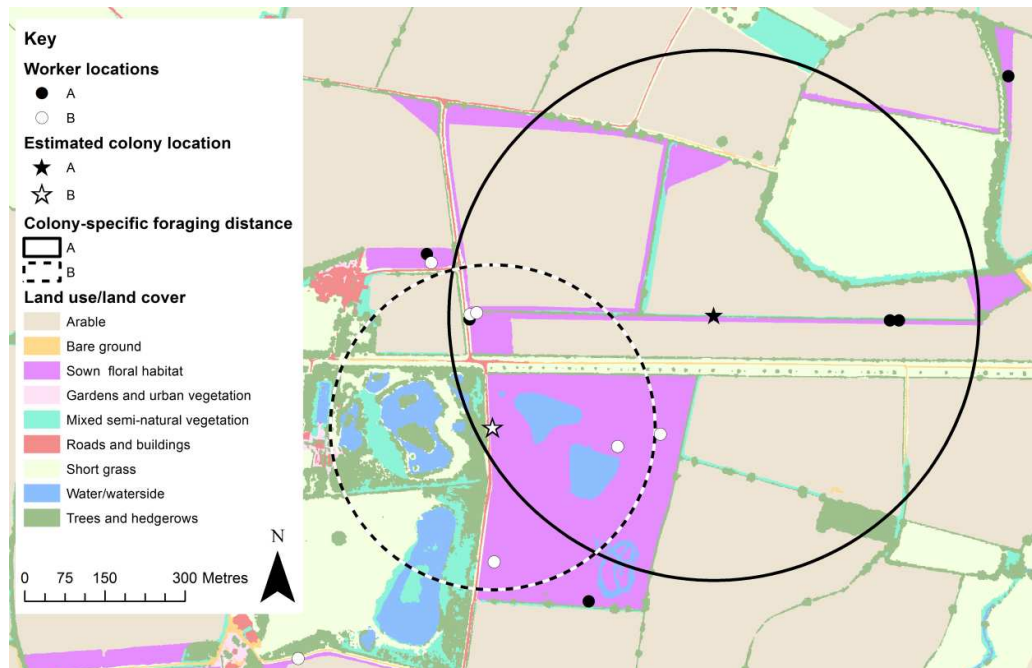
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557 **Table 2.** Results of linear regression of colony-specific foraging distance against log-transformed
 558 habitat variables, for five *Bombus* species. N = number of colonies. For land-use/land-cover classes,
 559 results are shown for only arable (AR) and mixed vegetation (MV) as these were the two variables
 560 showing statistical significance or high levels of model support. Floral cover variables are: total for
 561 all plant groups (ALL), non-crop (NC), worker-visited (WV) and worker-preferred (WP) species or
 562 groups. Landscape structure metrics are: mean edge area ratio (EA), mean shape index (SI) and
 563 hedgerow proximity index (HI). Asterisks denote significance at: * P < 0.05, ** P < 0.01, *** P < 0.001

		AR	MV	ALL	NC	WV	WP	EA	SI	HI	
<i>B. terrestris</i>	Slope	2.713	-2.096	0.420	-4.020	-4.092	-4.928	1.383	0.151	0.072	
	N = 65	R ²	0.327	0.072	-0.013	0.203	0.206	0.219	0.146	-0.016	-0.015
	DF = 63	p	<0.001***	0.017*	0.652	<0.001***	<0.001***	<0.001***	0.001***	0.891	0.831
		AIC	64.045	84.974	90.643	75.083	74.815	73.753	79.578	90.835	90.808
<i>B. lapidarius</i>	Slope	1.955	-3.469	0.061	-2.686	-2.581	-4.002	1.574	-0.450	0.520	
	N = 248	R ²	0.177	0.153	-0.004	0.063	0.058	0.085	0.189	-0.002	0.035
	DF = 246	p	<0.001***	<0.001***	0.873	<0.001***	<0.001***	<0.001***	<0.001***	0.474	0.002**
		AIC	216.108	223.190	265.328	248.298	249.448	242.182	212.363	264.835	255.401
<i>B. pascuorum</i>	Slope	3.396	-4.616	-0.930	-6.359	-6.341	-9.082	2.636	-3.601	0.754	
	N = 108	R ²	0.354	0.481	0.009	0.416	0.417	0.428	0.315	0.138	0.057
	DF = 106	p	<0.001***	<0.001***	0.165	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	0.008**
		AIC	109.362	85.621	155.535	98.483	98.227	96.128	113.511	138.127	147.682
<i>B. hortorum</i>	Slope	2.059	-4.411	-0.013	-4.294	-4.325	-7.339	1.252	-5.982	-0.368	
	N = 44	R ²	0.165	0.507	-0.024	0.253	0.256	0.383	0.084	0.205	0.001
	DF = 42	p	0.004**	<0.001***	0.986	<0.001***	<0.001***	<0.001***	0.032*	0.001**	0.312
		AIC	38.510	15.321	47.485	33.641	33.438	25.225	42.596	36.376	46.402
<i>B. ruderatus</i>	Slope	1.553	-3.034	-0.066	-4.849	-4.880	-13.590	2.661	-1.368	0.093	
	N = 41	R ²	0.143	0.373	-0.025	0.364	0.369	0.508	0.485	-0.007	-0.023
	DF = 39	p	0.009**	<0.001***	0.938	<0.001***	<0.001***	<0.001***	<0.001***	0.401	0.764
		AIC	18.607	5.788	25.968	6.360	6.086	-4.130	-2.294	25.224	25.878

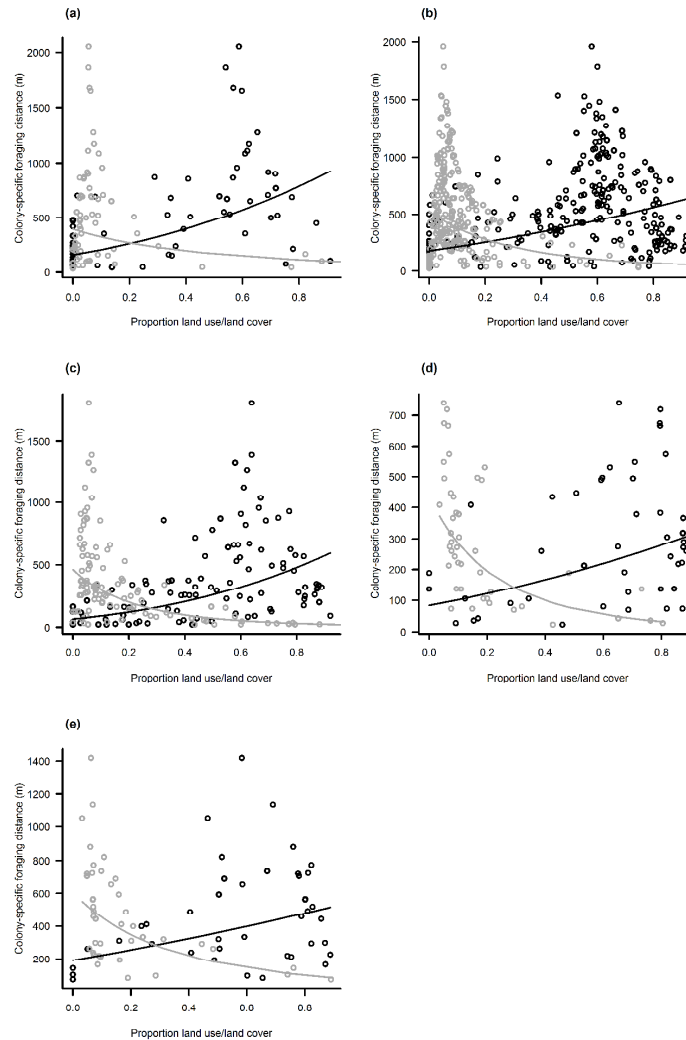
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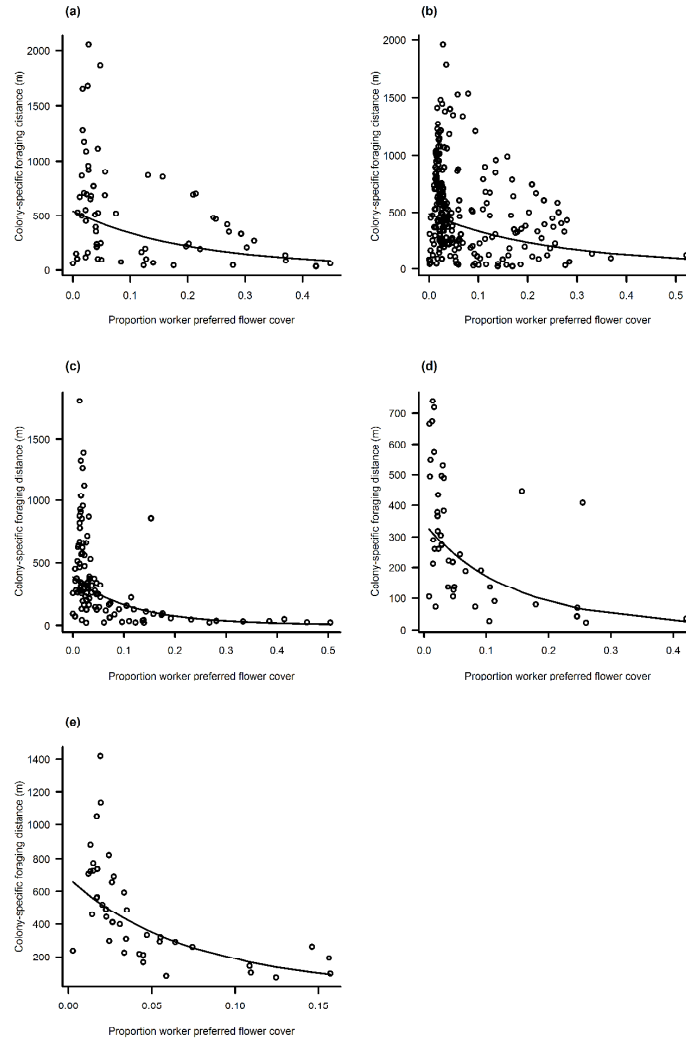
567 **Figure 1.** Example of the colony location estimation method, overlain on the land use/land cover
 568 map, for two bumblebee colonies (A and B). Black/white circular symbols = capture locations of
 569 workers determined to be from a given colony following genetic analysis. Stars = mean centres of
 570 these locations, i.e. estimated colony locations. Solid/dashed lines = buffers with a radius equal to
 571 the mean distance of all full sister workers to their estimated respective colony locations (i.e.
 572 'colony-specific foraging distance')



573

574 **Figure 2.** Plots of proportional cover of arable fields (black lines and symbols) and mixed vegetation
 575 (grey lines and symbols) against colony-specific foraging distance for five *Bombus* species; **(a)**
 576 *B. terrestris*, **(b)** *B. lapidarius* **(c)** *B. pascuorum* **(d)** *B. hortorum* **(e)** *B. ruderatus*. Trendlines back-
 577 transformed from linear regression of log transformed data (statistics in table 2).

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579

580 **Figure 3.** Plots of proportional cover of worker-preferred floral groups (specified in table S1) against
 581 colony-specific foraging distance for five *Bombus* species: **(a)** *B. terrestris*, **(b)** *B. lapidarius* **(c)**
 582 *B. pascuorum* **(d)** *B. hortorum* **(e)** *B. ruderatus*. Trendlines back-transformed from linear regression
 583 of log transformed data (statistics in table 2).

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587 **Supporting Information**

588 Additional Supporting Information may be found in the online version of this article:

589 **Fig. S1.** Map of the study landscape in Buckinghamshire, Southern England, UK, showing aggregate
590 land use/land cover classes derived from remote sensing data

591 **Table S1.** Plant groups used for field survey of habitat across the study landscape

592 **Table S2.** Results of Tukey post-hoc tests on bumblebee worker distance from colony, between all
593 possible pairs of study species

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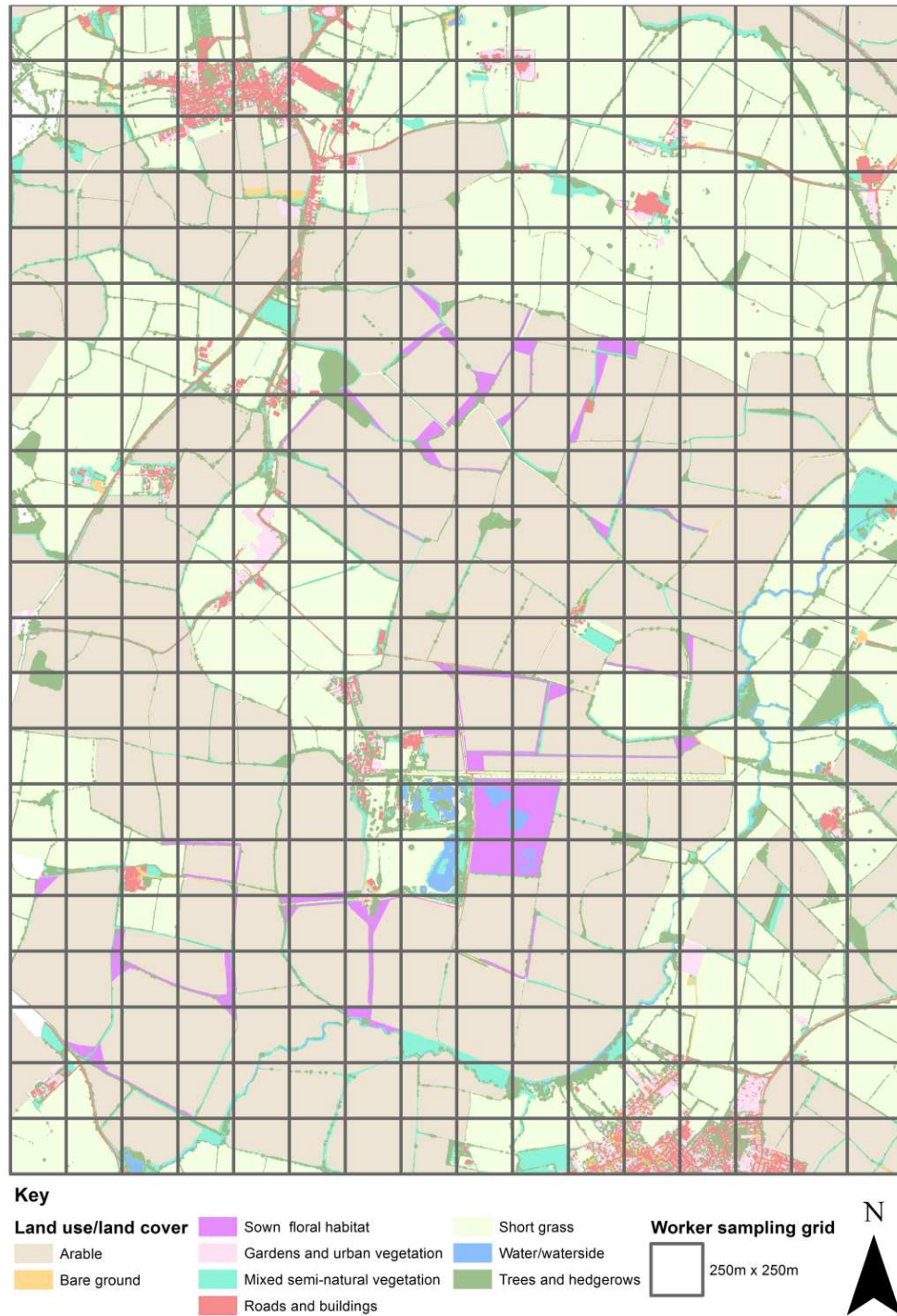


Fig. S1 Map of the study landscape in Buckinghamshire, Southern England, UK, showing aggregate land use/land cover classes derived from remote sensing data. Black grid lines represent 250 m x 250 m survey cells used to ensure full coverage of the study area for worker sampling and habitat surveys. Based on map in Dreier et al. (2014) with updated class descriptions and colour scheme.

Table S1. Plant groups used for field survey of habitat across the study landscape. Two measures of bumblebee visitation are given for the five *Bombus* study species - the percentage of foraging workers recorded on all species within each group and the mean number of worker visits per plant species within each group. Also given are the status of each group (Y = included, N = excluded) in the 'worker- visited' (i.e. visited by foraging workers during worker sampling) and 'worker-preferred' (i.e. the five plant groups with the highest mean number of visits per species) subsets.

Plant Group	Example Species	Percentage of foraging workers	Mean number of visits per species	Visited	Preferred
Red clover	<i>Trifolium pratense</i>	24.23%	592	Y	Y
White/Alsike clover	<i>Trifolium repens / hybridum</i>	32.71%	400	Y	Y
Lotus spp.	<i>Lotus corniculatus</i>	8.60%	210	Y	Y
Knapweeds, Scabious, Teasels	<i>Centaurea spp., Dipsacus fullonum</i>	12.20%	149	Y	Y
Other clovers	<i>Melilotus officinalis</i>	2.74%	67	Y	Y
Blue composites	<i>Cichorium intybus</i>	2.42%	59	Y	N
Other woody Rosaceae	<i>Rubus spp.</i>	1.92%	47	Y	N
Thistles	<i>Cirsium arvense, Carduus crispus</i>	3.44%	28	Y	N
Boraginaceae	<i>Borago officinalis</i>	1.64%	20	Y	N
White composites	<i>Leucanthemum vulgare</i>	2.42%	15	Y	N
Vetches	<i>Vicia spp., Lathyrus spp.</i>	2.29%	14	Y	N
Other Cruciferae	<i>Raphanus sativus</i>	1.06%	13	Y	N
Poppies	<i>Papaver spp.</i>	0.45%	11	Y	N
Ericaceae and <i>Lavendula</i>	<i>Erica spp., Lavendula spp.</i>	0.25%	6	Y	N
Lamiaceae and Scrophulariaceae	<i>Ajuga reptans, Ballota nigra</i>	1.68%	5	Y	N
Other fruiting/flowering tree	<i>Malus spp.</i>	0.16%	4	Y	N
Other woody species	<i>Buddleja davidii</i>	0.12%	3	Y	N
Rosaceae, non-woody	<i>Rosa spp.</i>	0.12%	3	Y	N
Others, non-woody	<i>Apiaceae, Violaceae,</i>	1.31%	2	Y	N
Yellow composites	<i>Taraxacum agg, Picris echioides</i>	0.25%	2	Y	N
Cereals	<i>Triticum aestivum, Zea mays</i>	0.00%	0	N	N
Convolvulaceae	<i>Calystegia sepium</i>	0.00%	0	N	N
<i>Crataegus</i> spp.	<i>Crataegus monogyna</i>	0.00%	0	N	N
Field bean	<i>Vicia faba</i>	0.00%	0	N	N
Gorse	<i>Ulex europeaus</i>	0.00%	0	N	N
Oilseed rape	<i>Brassica napus</i>	0.00%	0	N	N
<i>Prunus</i> spp.	<i>Prunus spinosa</i>	0.00%	0	N	N
<i>Salix</i> spp.	<i>Salix caprea</i>	0.00%	0	N	N

Table S2. Results of Tukey post-hoc tests on bumblebee worker foraging distance, between all possible pairs of study species. Mean foraging distances shown in parentheses. Tests show that species can be split into 'shorter' and 'longer' range foragers. Asterisks denote significance at: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS, not significant.

	<i>B. lapidarius</i> (536)	<i>B. pascuorum</i> (337)	<i>B. hortorum</i> (273)	<i>B. ruderatus</i> (502)
<i>B. terrestris</i> (551)	0.953 NS	<0.001 ***	<0.001 ***	0.932 NS
<i>B. lapidarius</i> (536)		<0.001 ***	<0.001 ***	0.998 NS
<i>B. pascuorum</i> (337)			0.997 NS	<0.001 ***
<i>B. hortorum</i> (273)				<0.001 ***