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# On the verge? Preferential use of road-facing hedgerow margins by bumblebees in agro-ecosystems

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1  **Abstract**

2   The global pollinator decline is commonly linked to modern intensive farming

3   practices, partly because excessive herbicide and fertilizer use is thought to reduce

4   pollinator food plant availability. This effect is particularly obvious across crop- /non-

5   crop boundaries, but no study has compared pollinator and food plant abundance on

6   adjacent crop- and roadside margins. We compared bumblebee abundance along 30

7   hedgerows in SW England; bordered either side by roads and arable fields (cultivated

8   with wheat, barley, oilseed rape, or beans). Total bumblebee abundance along roadsides

9   was over twice that observed on adjacent crop-facing margins, irrespective of crop type

10  and this general pattern was apparent for three of the five most common bumblebee

11  species, including generalist and specialist foragers. Both the total number of flowering

12  plant species and the floral abundance of three of the five most visited plants was also

13  higher on roadsides; minor variation between crops was localised and unrelated to

14  margin orientation. We conclude that organic farming may offer some advantages for

15  pollinator conservation since it reduces field margin exposure to agro-chemical inputs.

16  However, since conventional farming will remain central to global food production,

17  modifications to current practices (such as the use of wildflower strips) are needed and

18  may have ancillary benefits for pollinators by protecting arable margins from

19  disturbance and agro-chemicals. In addition, the fact that the roadsides were

20  demonstrably better habitats for pollinators and their food plants than field-facing

21  margins underscores the widespread suggestion that roadside verges should be utilised

22  more as a conservation tool to promote pollinator biodiversity.

**Introduction**

26   The global decline of many different insect pollinators is now well established and the

27   potential repercussions for crop and wildflower pollination widely discussed (Ghazoul

28   2005; Gallai et al. 2009; Potts et al. 2010; Vanbergen et al. 2013). The likely causes of

29   pollinator declines are numerous, but centre around habitat loss and fragmentation

30   (Goulson et al. 2005; Winfree et al. 2009), the direct and indirect impacts of pesticide

31   use (Brittain and Potts 2011; Whitehorn et al. 2012), and related implications for

32   immune-competence and increased susceptibility to disease (Cameron et al. 2011;

33   Whitehorn et al. 2011). Each of these factors can be linked to the recent, large-scale

34   intensification of agricultural production (Vanbergen et al. 2013). Although all insect

35   pollinator groups have been affected to some extent, bees and bumblebees (*Bombus*

36   species) in particular, are perhaps the most emblematic of the causes and likely

37   consequences of recent pollinator losses. Within the UK for example, three out of the 25

38   known *Bombus s*pecies are now extinct and a further eight have experienced major

39   contractions in distribution and abundance (Goulson et al. 2005) and the UK situation is

40   mirrored globally (Goulson and Hanley 2004; Williams and Osborne 2009; Cameron et

41   al. 2011). The loss of any pollinator has potentially negative consequences for effective

42   ecosystem service provision (Ollerton et al. 2011), but by virtue of their ability to

43   pollinate a large proportion of crop plants and wildflowers, and do so in climatic

44   conditions that other pollinators cannot tolerate, bumblebee decline is of particular

45   concern in temperate regions (Goulson 2010).

46   Recognising that any attempt to halt or reverse bumblebee losses has to be achieved

47   within the context of highly-modified agricultural landscapes, and continued economic

48   and societal pressure to maximise food production, many contemporary conservation

49  options focus on modification to existing farming practices. Consequently the subsidy

50  of cultivated wildflower strips and low input pasture to increase food plant availability

51  became successful pillars of agri-environment schemes (Albrecht et al. 2007; Carvell et

52  al. 2007; Breeze et al. 2014). There are however, other ways in which modification of

53  current farming practices can support bumblebees. By virtue of providing a large and

54  concentrated floral resource, mass flowering crops such as oilseed rape (canola),

55  sunflowers, and beans attract and support bumblebees (Westphal et al. 2003; Hanley et

56  al. 2011; Stanley and Stout 2013). Organic farming is frequently associated with

57  increased bumblebee abundance, not only because of reduced toxicological impacts of

58  agro-chemicals on the insects, but also because of the associated increase in the

59  diversity and abundance of food plants (Belfrage et al. 2005; Holzchuh et al. 2007).

60  However, only a relatively small proportion of cultivated land is currently under organic

61  agriculture and the likely future contribution to global food demand is widely debated

62  (Connor, 2008; Seufert et al. 2012). The situation is complicated further as some authors

63  suggest that the link between organic farming and enhanced biodiversity may simply

64  reflect lower crop yield, since some high productivity organic systems appear to be no

65  more beneficial to wildlife than their conventional counterparts (Gabriel et al. 2013; but

66  see Tuck et al. 2014).

67  As the largest component of semi-natural habitats in Europe and North America

68  (Marshall and Moonen 2002), arable field margins are vital for maintaining bumblebee

69  populations. Even in the most intensively farmed systems, hedgerows, headlands, and

70  ditches provide at least some pollen and nectar forage in addition to opportunities for

71  nesting and hibernation sites (Mänd et al. 2002; Goulson et al. 2008; Hannon and Sisk

72  2009). Although found in many parts of NW Europe (e.g. the *Bocage* of Normandy),

73    hedgerows are particularly common in the British Isles and feature prominently in UK

74    conservation planning (e.g. Environmental Stewardship Schemes – see Merckx et al.

75    2009; Staley et al. 2012). There is concern however, that the range of agro-chemicals

76    routinely used in conventional farming impact severely upon the ability of arable field

77    margins to support biodiversity. Pesticide drift is a major problem, not only because

78    insecticides reduce bee survival and growth (Whithorn et al. 2012; Baron et al. 2014),

79    but also because of the negative impact on pollinator food plants (Marrs et al. 1989;

80    Schmitz et al. 2014). The use of inorganic fertilizers also has significant repercussions

81    for the composition of arable margin flora; elevated soil nitrogen levels promoting the

82    growth of highly competitive grasses at the expense of subordinate, herbaceous food

83    plants used by pollinators (Tsiouris and Marshall 1998; De Cauwer et al. 2006; Schmitz

84    et al. 2014).

85    In addition to providing habitat and corridors for biodiversity however, hedgerows can

86    also act as a filter for agro-chemical inputs. Tsiouris and Marshall (1998) report a

87    dramatic reduction in soil nitrogen concentration from the side of a hedgerow facing an

88    arable field to the opposite 'control' side, while Otto et al. (2009) show a similar effect

89    for pesticides. This effect is however, only likely to be apparent where one side of the

90    hedgerow does not routinely receive pesticide or fertilizer input, a situation most

91    commonly encountered when the arable field borders a road. Using this rationale,

92    Croxton et al. (2002) compared the plant and bumblebee communities either side of

93    hedgerows bordered by arable fields (wheat or oilseed rape) and green lanes (un-

94    metalled tracks used primarily by walkers and horse-riders). They showed that plant

95    species richness and bumblebee abundance were higher on the side adjacent to the green

96    lane, although they recognised that their results may have been partly confounded by the

97    fact that the central portion of the lane also contains pollinator food plants. Nonetheless,

98    similar variation in the abundance of bee food plants was reported by Henriksen and

99    Langer (2013) when they examined paired road and arable (wheat) margins in

100   Denmark. To date however, no study has compared bumblebee abundance across

101   hedgerows bordering sealed roads and arable fields containing multiple crop types.

102   The main aim of this study was to test the hypothesis that bumblebee abundance and

103   species composition vary across arable field - road boundaries, irrespective of the crop

104   being cultivated. Although disturbance and exposure to vehicular emissions might be

105   expected to have negative impacts on biodiversity (Forman and Alexander 1998;

106   Spellerberg 1998), many country roads experience relatively low traffic volumes and we

107   hypothesised that by virtue of the presence of hedgerows common in our study region,

108   road verges would offer enhanced forage opportunities for bumblebees. In addition,

109   there is a growing movement to use roadside verges as a means of promoting pollinator

110   habitat and abundance (Hopwood 2008; Noordijk et al. 2009; Wojcik and Buchmann

111   2012; Skórka et al. 2013) and our study offers a way of assessing the comparative value

112   of roadside verges for pollinators and their food plants.

113   **Materials and Methods**

114   *Study sites*

115   Bumblebee surveys were carried out over a 5-week period between early June and

116   early-July 2013 in 30 paired arable field and adjacent roadside margins situated in

117   Devon and Cornwall, southwest England (Table S1). All sites were situated amongst

118   intensively farmed, mixed arable and pastoral field systems typical of the region, and

119   were well away from other major land-use types (forestry, upland moorland) and major

120   urban conurbations (Plymouth, Torbay, and Exeter). Consequently, it is unlikely that

121   variation in land-use at the landscape-scale had any impact on bumblebee assemblages

122   around our chosen study sites. In addition all fields were between 50m and 190m absl

123   and we included a mixture of field and (crop-facing) margin aspects in our surveys such

124   that our observations were not biased by field/margin aspect or altitude (Table S1). All

125   margins were centred on long-established (i.e. > 200 years) hedgerows comprised of

126   several native woody plant species; e.g. *Corylus avellana* L., *Crataegus monogyna*

127   Jacq. *Fraxinus excelsior* L., *Prunus spinosa* L. *Rosa canina* L., *Rubus fruticosus* L., and

128   *Ulex europaeus* L. and which typically possess a naturally colonising, diverse basal

129   flora including *Dactylis glomerata* L., *Digitalis purpurea* L., *Geranium robertianum* L.,

130   *Heracleum sphondylium* L., *Ranunculus repens* L., *Silene dioica* (L.) Clairv., *Stachys*

131   *sylvatica* L., and *Urtica dioca* L. Typically both road- and field-facing hedgerows and

132   margins are cut once a year (in mid/late-summer) with little or no other deliberate

133   management. Consequently the trajectory of plant community development either side

134   of field boundaries likely reflects modification of a common basal flora by agro-

135   chemical input and disturbance on the field-side and (to lesser extent given low traffic

136   volumes) disturbance and exhaust fume emissions on the road-side.

137   While we were unable to ascertain a detailed account of pesticide use for study sites,

138   each land-owner confirmed that all arable fields had been in conventional cultivation for

139   several decades and were thus likely to have experienced a long history of exposure to

140   agro-chemicals. In addition, the structural similarity of the field margins, coupled with

141   the fact that all the arable crops we encountered are planted in rotation, means that crop-

142   type or associated agro-chemical application within individual farms were unlikely to

143   affect the location and abundance of bumblebee nests or hibernation sites, or plant

144    community composition. We focussed on four arable crops; wheat (*Triticum aestivum*

145    L.), barley (*Hordeum vulgare* L.), oilseed rape (*Brassica napus* L.) and field bean (*Vicia*

146    *faba* L.), which together account for 46%, 23%, 18% and 2% (by area) respectively of

147    all arable crops grown in the UK (Garthwaite et al. 2012). The use of replicate wheat

148    (9), barley (8), bean (7) and oilseed rape (6) fields also allowed us to compare whether

149    any variation in bumblebee assemblages between field- and roadside margins was

150    linked to crop type. All fields were separated by at least 1 km to minimize non-

151    independence of observed bumblebees (Knight et al. 2005; Osborne et al. 2008).

152    *Bumblebee surveys*

153    At each location we monitored bumblebee activity along a $100 \times 2m$ transect set out

154    along the central part of an arable field margin, and matched this with an adjacent road-

155    side margin. UK agricultural policy requires a 1m border between the field boundary

156    and the crop edge, and for our arable fields this border was comprised primarily of the

157    perennial herb and grass species associated with the basal flora of the hedgerow. This

158    1m border, plus an additional metre extending to a point approximately half way into

159    the hedgerow proper, formed the 2m width of our transects on the arable field margin.

160    All adjacent road-side verges were selected such that 1m of verge was available running

161    from the hedgerow base to provide a mirror sample to the arable side.

162    Transects were walked once between 9:00-17:00 on days favourable to bumblebee

163    activity (Goulson and Darvill 2004). Each transect took approximately 15 minutes to

164    complete, with a 15 minute 'rest' period between sides to limit repeat sampling of

165    individual bees before the adjacent margin was sampled. We identified and recorded all

166    bumblebees observed actively foraging (i.e. actually visiting an inflorescence), together

167    with the plants upon which they foraged. Due to the difficulty of separating workers of

168    the subgenus *Bombus* s. str. (i.e. *Bombus terrestris* (L.), *B. lucorum* (L.), *B. magnus*

169    Vogt. and *B. cryptarum* (Fabricius) in the field (Williams et al. 2012), we made no

170    attempt to distinguish between these species and throughout refer to this group

171    collectively as *B. terrestris* agg. We made no attempt to capture foraging bumblebees,

172    but because transects were linear and completed relatively rapidly, it is extremely

173    unlikely that the same individual was recorded more than once during each transect

174    walk.

175    Immediately after completing bumblebee surveys, we estimated the number of flowers

176    of each plant species likely to be visited by bumblebees along each transect to determine

177    variation in floral resource availability between field- and roadside margins. Estimates

178    for total flower number were achieved by counting the number of flowers on 10

179    separate inflorescences of a given plant species and then to multiply this mean value by

180    the estimated total number of inflorescences observed along the transect. For Asteraceae

181    a capitulum was considered to be a single 'flower'.

182    Following an Anderson-Darling test for normality and data transformation where

183    appropriate, we compared variation in total bumblebee visitation to road- and crop-

184    facing margins using a General Linear Model (GLM) with 'margin orientation' and

185    'crop' as factors and the 'margin orientation' ×'crop' interaction to examine evidence

186    for crop-specific variation in bumblebee response to margin orientation. The same

187    approach was applied individually to each of the five most commonly visited plant

188    species. All analyses were performed in Minitab version 16.0.

189

## Results

In total we observed 211 bumblebees foraging along hedgerow transects; the majority of which (70%) were recorded on the roadside margin (Fig 1). We also observed some variation between crops; barley field margins attracting on average over twice the number of bumblebees (mean per transect = 4.9 ± 0.8SE) as beans (2.4 ± 0.3). A two-factor GLM confirmed the strong effect of 'margin orientation' ($F_{1,52}$ = 27.7, $P$ = <0.001) and 'crop' ($F_{3,52}$ = 4.42, $P$ = 0.008) on bumblebee abundance. However, there was no 'margin orientation' ×'crop' interaction ($F_{3,52}$ = 3.50, $P$ = 0.458), suggesting that the higher abundance of bumblebees on roadside margins remained consistent for all four crops.

The majority of forage visits were made by *B. terrestris* agg. (44.1% of total bumblebee visits), followed by *B. hortorum* L. (16.6%), *B. pascourum* Scopoli (16.6%), *B. lapidarius* L. (11.4%), *B. pratorum* L. (9.0%), and *B. hypnorum* (L.) (2.4%). A Chi-square test of association found no significant difference ($\chi^2$ = 10.58, df = 5, $P$ = 0.06) in the relative frequency of the six *Bombus* species foraging on roadside or crop-facing margins. Nonetheless, three species (*B. terrestris, B. hortorum* & *B. pratorum*) were more frequent on the road-side margin with none of these yielding a significant 'margin orientation' ×'crop' interaction (Table 1).

A total of 22 different plant species were visited by bumblebees during the surveys and on average more flowers of these species were available to bumblebees on roadside verges than those facing the crop (Two-factor GLM: 'margin orientation' $F_{1,52}$ = 5.18, $P$ < 0.027). However, neither the 'crop' ($F_{3,52}$ = 2.25, $P$ = 0.094) effect nor the 'margin orientation' × 'crop' interaction ($F_{3,52}$ = 0.71, $P$ = 0.533) were significant (Fig 2).

213    The five most frequently visited plant species were *Silene dioica* (38.4% of bumblebee

214    visits), *Heracleum sphondylium* (20.4%), *Geranium robertianum* (11.8%), *Digitalis*

215    *purpurea* (9.5%), and *Ranunculus repens* (9%), together accounting for 89% of all

216    recorded visits. Of these, the flowers of *S. dioica* (two-factor GLM on $\log_{10}$ transformed

217    data - $F_{1,52} = 4.69$, $P = 0.035$), *G. robertianum* ($F_{1,52} = 16.35$, $P < 0.001$), and *R. repens*

218    ($F_{1,52} = 31.04$, $P < 0.001$) were more abundant on roadside margins (Fig 3). Two

219    species, *G. robertianum* ($F_{3,52} = 2.91$, $P = 0.043$) and *H. sphondylium* ($F_{3,52} = 4.78$, $P =$

220    0.005) exhibited variation linked to crop type, likely reflecting the high relative

221    abundance of the former in wheat margins and of the latter in barley. However, none of

222    the five species examined showed any 'margin orientation' ×'crop' interaction,

223    suggesting where plant species had higher floral abundance on roadside margins, the

224    effect was consistent across all crop types.

225    **Discussion**

226    Our results revealed that foraging bumblebees were more abundant along roadside

227    margins of arable field boundaries; an observation consistent for three of the most

228    common UK bumblebees and including species considered to be both generalist (*B.*

229    *terrestris* agg and *B. pratorum*) and specialist (*B. hortorum*) foragers. At the same time,

230    road-side margins offered more abundant floral resources for pollinators than the

231    adjacent crop-facing margin. Given the close relationship between forage plant

232    availability and bumblebee abundance (Heard et al. 2007; Hanley et al. 2014), it seems

233    reasonable to conclude that that the higher floral abundance on roadside margins was

234    responsible for elevated bumblebee numbers. Although we made no attempt to quantify

235    soil nitrogen or pesticide, a number of studies have shown marked variation in agro-

236    chemical concentrations just meters across arable field margins (Tsiouris and Marshall

237   1998; Croxton et al. 2002; Otto et al. 2009). It is likely that there was some deposition

238   of nitrous oxides from car exhausts along our roadside margins, although recent

239   evidence from North America (Bettez et al. 2013; Watmough et al. 2014) suggests that

240   for even busy roads (i.e. a traffic volume of several thousand cars per day), annual

241   roadside nitrogen deposition is at least two orders of magnitude lower than levels

242   associated with agricultural inputs on crop-facing margins (Tsiouris and Marshall

243   1998). Consequently it likely that the across-hedgerow variation in flowering plant

244   species abundance we observed for relatively low traffic volume countryside roads was

245   linked to variation in soil nitrogen levels (see Tsiouris and Marshall 1998; De Cauwer et

246   al. 2006; Schmitz et al. 2014), although additional impacts of herbicide application and

247   disturbance (ploughing) are probable (Croxton et al. 2002). Indeed, Marrs et al. (1989)

248   showed that the local effects of herbicide spray drift can be lethal for both *S. dioica* and

249   *D. purpurea*, two of the most important bumblebee forage species observed in our

250   study.

251   We also found remarkably little between-crop variation for either bumblebee or food

252   plant abundance. Only *Bombus terrestris* agg exhibited any variation linked to crop type

253   (being more abundant in barley margins) which may itself be explained in part by the

254   higher relative abundance of *H. sphondylium* flowers. Like *G. robertianum* in wheat,

255   where 35% of all recorded flowers for all crops were located along four hedgerows,

256   49% of all *H. sphondylium* flowers were recorded from five barley margins.

257   Consequently the apparent concentration of *B. terrestris* agg on barley probably reflects

258   local patchiness in forage availability rather than any variation due to the crop type itself

259   (11 of the 18 observations of *B. terrestris* agg on *H. sphondylium* were from these sites).

260   The fact that we found no 'margin orientation' ×'crop' interactions for individual bee or

261    plant species highlights the remarkable consistency in our results and corroborates our

262    conclusion that consistently higher floral abundance on roadside margins supported

263    more bumblebees, irrespective of the adjacent crop type.

264    Although Henriksen & Langer (2013) also showed that flowers of likely bumblebee

265    food plants were more abundant on the roadside margin of arable field boundaries, they

266    did not investigate the associated impact on the pollinator community. Croxton et al.

267    (2002) did report a positive association between plant and bumblebee communities

268    along track-sides, but their study focussed on green-lanes and investigated just two

269    different crop types (wheat and oilseed rape). Consequently ours is the first study to

270    show how (sealed) roadside margins support comparatively more bumblebees and their

271    food plants in comparison with adjacent crop-facing margins. This is important because

272    unlike green-lanes that offer forage resources within the lane itself, sealed roadside

273    margins offer a more robust control against which to compare the impacts of

274    conventional farming practices on the pollinator assemblages of arable field margins

275    (Croxton et al. 2002).

276    We recognise that we did not look at landscape- or even farm-scale impacts, but the fact

277    that bumblebee abundance varied so markedly between crop-facing and roadside

278    margins corroborates the widely-held view that conventional farming practices are

279    culpable (in this case via impacts on food plants) for recent pollinator losses (Goulson et

280    al. 2005; Brittain and Potts 2011; Cameron et al. 2011; Vanbergen et al. 2013). Farming

281    policy and practice is changing however. Recent schemes that encourage farmers to

282    cultivate or re-instate the flower-rich hay meadows required by many pollinators

283    (Goulson et al. 2005; 2006) are welcome, but when set against the global demand for

284    food, other options must be considered. Our results corroborate the view that by virtue

285  of reduced agro-chemical inputs (and noting that our design eliminates the potentially

286  confounding impacts of crop yield identified by Gabriel et al. (2013)), organic farming

287  could benefit the floral abundance of arable field margins and so promote forage

288  availability for pollinators. Nevertheless, any significant increase in the contribution of

289  organic farming to future global food supply remains in doubt (Connor 2008; Seufert et

290  al. 2012) and modifications to conventional farming methods seem the most likely way

291  to halt further pollinator losses. Due to the widening use of agri-environment schemes,

292  many such measures are already in place, but our results further underscore their

293  potential for pollinator conservation. Wildflower mixtures sown along arable field

294  margins are widely thought to benefit pollinators such as bumblebees by increasing

295  forage availability (Carvell et al. 2007; Pywell et al. 2011), but a further advantage is

296  that they provide a buffer against disturbance and agro-chemical input that may also

297  encourage pollinator-friendly plant species within the permanent field margin (see Kells

298  et al. 2001). Although these measures entail some loss of potential cropping area,

299  further benefits accrue to farmers if a minor reduction in crop yield is compensated by

300  increased pollinator service provision to crops (Breeze et al. 2014; Manning et al.

301  2014).

302  Our results also underscore the wider value of roadside verges for pollinator

303  conservation. Not only do roadsides provide refuge from intensive farming practices,

304  when taken together they offer considerable habitat potential; equivalent to over

305  236,000 Ha in the UK and over 3-million Ha in the USA (Wojcik and Buchmann 2012).

306  It is likely that even without any specific management, much of the available roadside

307  capacity in the UK already provides suitable pollinator habitat; this certainly seems to

308  be the case in our study. Moreover, it must be remembered that in addition to floral

309   rewards, in order for them to be attractive to bumblebees roadsides and adjoining areas

310   must also offer nesting and hibernation sites. Again, this is true of our field margins

311   since they were comprised exclusively of mature hedgerows. However, restoring

312   degraded or intensively managed (sub-)urban roadsides to encourage native, flower-rich

313   vegetation could benefit pollinator conservation particularly if nesting and hibernation

314   sites are available.

315   **Acknowledgements**

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467    **Figure Legends**

468    **Fig. 1.** Variation in mean (± SE) bumblebee abundance along 100m long

469    transects located either side of adjacent arable field margins (crop-facing versus

470    roadside). Observations were made along 100m hedgerow transects situated

471    next to one of four different crop types in 30 conventionally-farmed fields in SW

472    England.

473

474    **Fig. 2.** Variation in mean (± SE) abundance of all bumblebee forage plant

475    species along 100m long transects located either side of adjacent arable field

476    margins (crop-facing versus roadside). Observations were made along 100m

477    hedgerow transects situated next to one of four different crop types in 30

478    conventionally-farmed fields in SW England.

479

480    **Fig. 3.** Variation in mean (± SE) floral abundance of the five most frequently

481    used bumblebee forage plants along 100m long transects located either side of

482    adjacent arable field margins (crop-facing versus roadside). Observations were

483    made along 100m hedgerow transects situated next to one of four different crop

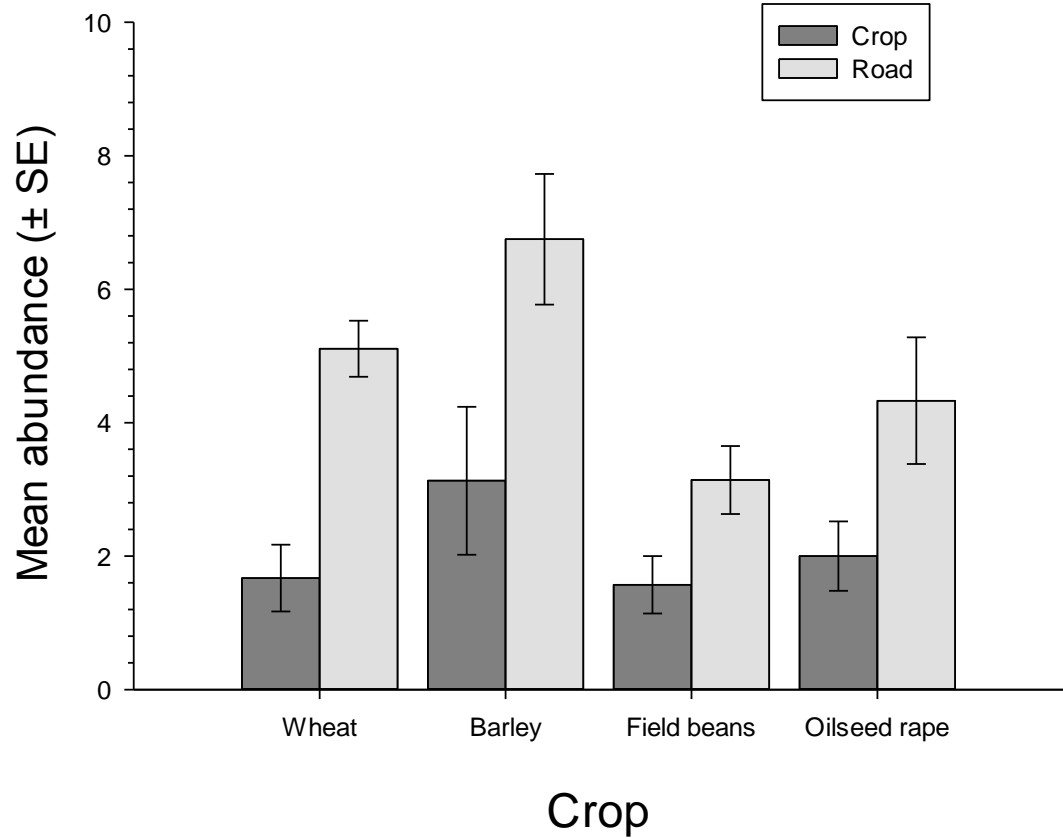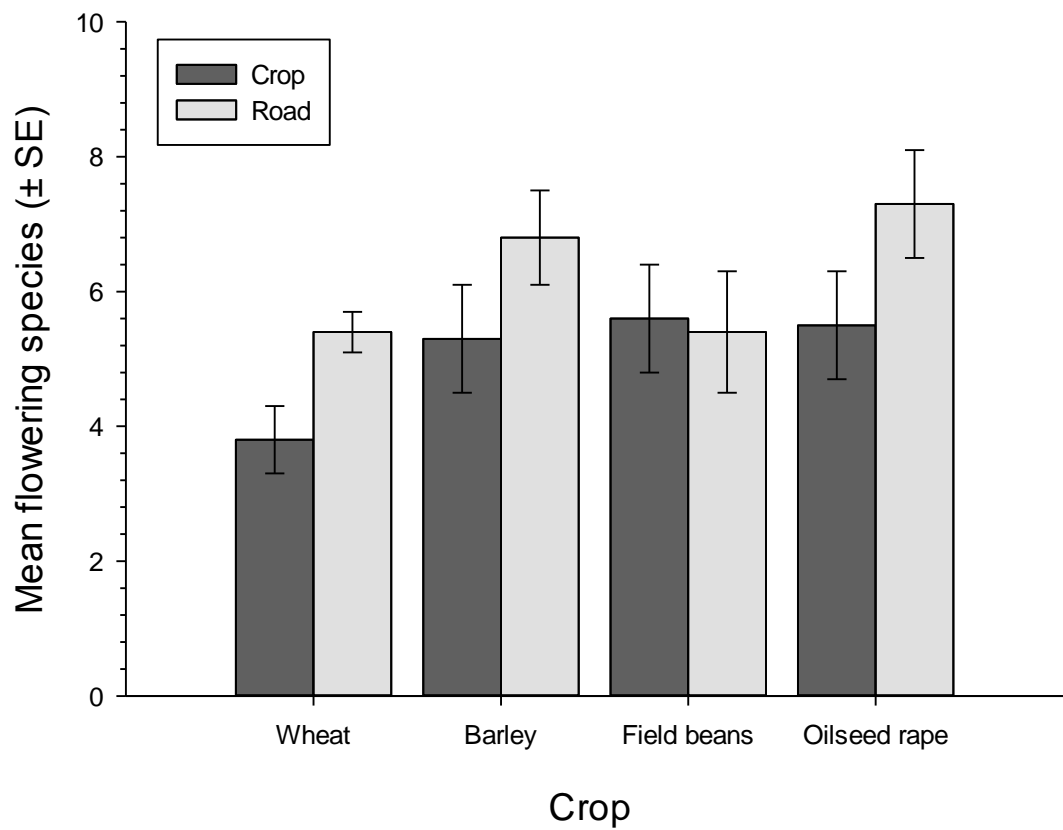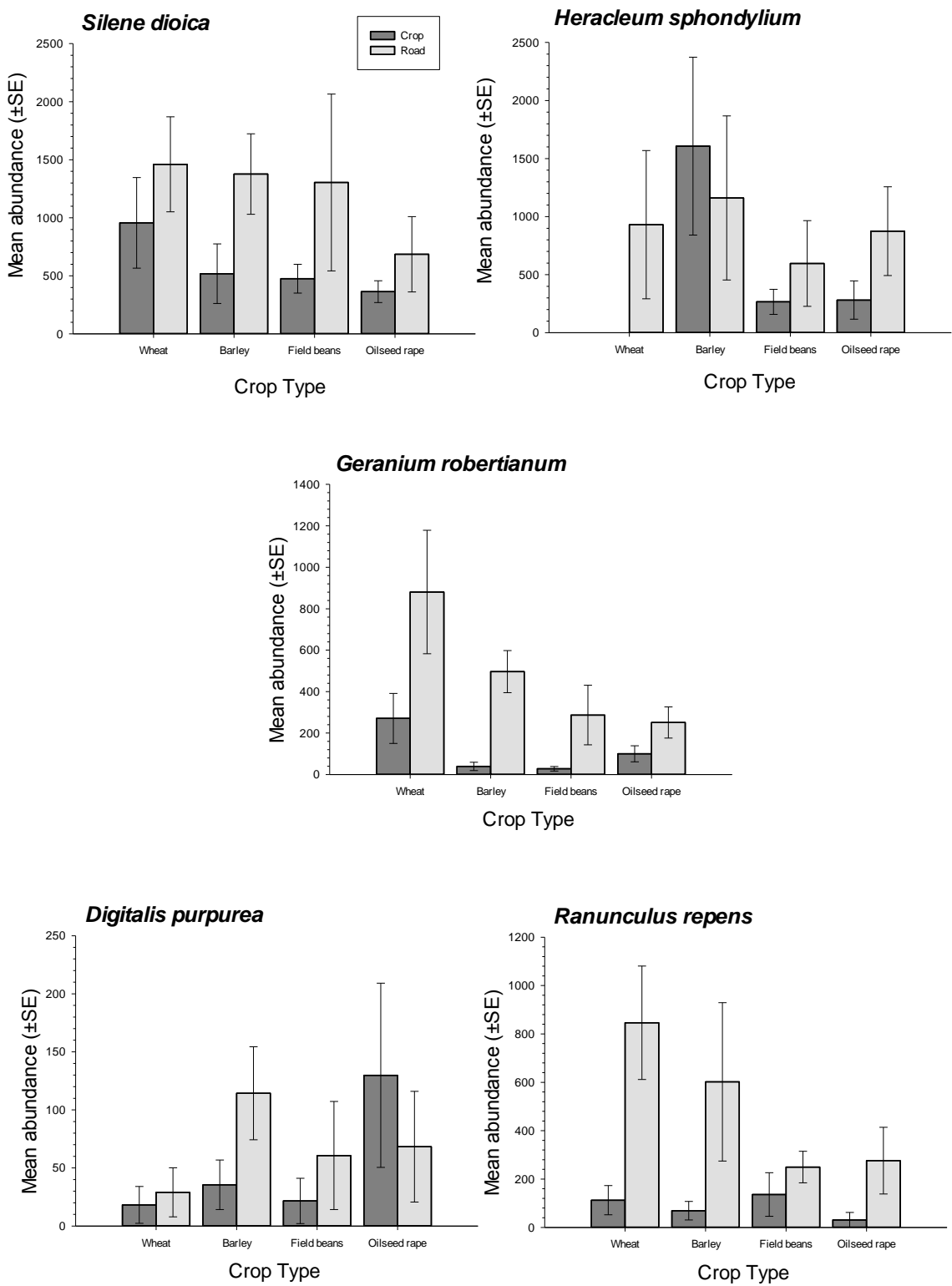484    types in 30 conventionally-farmed fields in SW England.

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488   Fig 1

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501    Fig 2

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506    Fig 3

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511    **Table 1.** Variation in mean (± SE) abundance of five bumblebee species observed foraging

512    along adjacent 100m hedgerow transects either side of arable field margins (crop-facing versus

513    roadside) situated next to one of four different crop types in 30 conventionally-farmed fields in

514    SW England. Results of a two-factor General Linear Model examining the interactive effects of

515    margin orientation and crop type are shown; emboldened '*P*'-values denote $P < 0.05$. In addition

516    to the species shown, a further five individuals of *Bombus hypnorum* were recorded.

517

| Crop | Margin orientation | *B. terrestris* (93 bees) | | *B. hortorum* (35 bees) | | *B. pascourum* (35 bees) | | *B. lapidarius* (24 bees) | | *B. pratorum* (19 bees) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| Wheat | Crop | 0.78 | 0.43 | 0 | 0 | 0.33 | 0.17 | 0.33 | 0.17 | 0.11 | 0.11 |
| | Road | 1.78 | 0.28 | 1.00 | 0.29 | 1.33 | 0.41 | 0.67 | 0.24 | 0.33 | 0.17 |
| Barley | Crop | 1.38 | 0.53 | 0.50 | 0.27 | 0.75 | 0.41 | 0 | 0 | 0.25 | 0.16 |
| | Road | 3.63 | 0.56 | 1.38 | 0.42 | 0.75 | 0.41 | 0.71 | 0.34 | 0.38 | 0.18 |
| Beans | Crop | 0.86 | 0.26 | 0.14 | 0.14 | 0.43 | 0.20 | 0.14 | 0.14 | 0 | 0 |
| | Road | 1.43 | 0.20 | 0.29 | 0.18 | 0.29 | 0.18 | 0.14 | 0.14 | 0.83 | 0.44 |
| Oilseed rape | Crop | 0.83 | 0.31 | 0 | 0 | 0.17 | 0.17 | 1.00 | 0.37 | 0 | 0 |
| | Road | 1.50 | 0.56 | 1.33 | 0.76 | 0.33 | 0.21 | 0.33 | 0.21 | 0.83 | 0.31 |
| All crops | Crop | 3.22 | 1.04 | 0.56 | 0.24 | 1.44 | 0.47 | 1.11 | 0.31 | 0.33 | 0.17 |
| | Road | 7.11 | 1.02 | 3.33 | 0.71 | 2.44 | 0.60 | 1.56 | 0.18 | 1.78 | 0.52 |
| **GLM results** | | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* |
| Orientation $_{(DF = 1,52)}$ | | 13.76 | **0.001** | 13.55 | **0.001** | 1.30 | 0.259 | 0.21 | 0.645 | 10.35 | **0.002** |
| Crop $_{(DF = 3,52)}$ | | 4.93 | **0.004** | 1.81 | 0.157 | 1.64 | 0.192 | 1.91 | 0.140 | 0.32 | 0.812 |
| Orientation × Crop $_{(DF = 3,52)}$ | | 1.69 | 0.180 | 1.12 | 0.350 | 1.50 | 0.227 | 2.87 | **0.045** | 1.40 | 0.253 |

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