



Landscape structure influences pollinator movements and directly affects plant reproductive success

Louise Cranmer, Duncan McCollin and Jeff Ollerton

L. Cranmer, D. McCollin and J. Ollerton (jeff.ollerton@northampton.ac.uk), School of Science and Technology, Univ. of Northampton, Avenue Campus, Northampton, NN2 6JD, UK. JO also at: Landscape and Biodiversity Research Group, School of Science and Technology, Univ. of Northampton, Avenue Campus, Northampton, NN2 6JD, UK.

Pollinators play a key role within most terrestrial communities in maintaining plant populations, as well as pollinating many agricultural crops for seed and fruit production. The mobility of pollinating animals is significant to their importance but we know little about how landscape structure influences pollinator movements. Linear landscape features such as hedgerows and embankments are conspicuous features of agricultural landscape structure and are important artificial habitats in their own right. However, there has been some debate as to the function of these landscape elements as corridors between larger expanses of semi-natural habitat separated by urban and agricultural habitats. Few studies have specifically studied insect flight responses to linear landscape elements. By observing bumblebee flight behaviour along hedgerows and, by creating a medium-scale experimental array of flower patches using an artificial linear feature, we examined whether such structures can elicit an oriented flight response along them and therefore facilitate insect movement through the landscape. We found that both hedgerows and artificial linear landscape features can influence the flight directions of bumblebees (*Bombus* spp. Hymenoptera, Apidae), one of Europe's most important groups of pollinators. A bioassay experiment in which *Salvia pratensis* (Lamiaceae) was planted into landscape patches with differing numbers of connecting hedgerows showed that this directional response can have a profound effect on plant reproductive success – plants had increased pollinator activity, pollen receipt and subsequent seed set in patches with more connections. The overall hedgerow connectedness of a landscape is therefore important both to bumblebee movement and to those plants which depend on bumblebees for pollination services.

Biotic pollination of plants is fundamental to the continued functioning of most terrestrial ecosystems (Kearns et al. 1998, Waser and Ollerton 2006, Ollerton et al. 2011). However pollination interaction webs throughout the world have suffered from various anthropogenic perturbations from agricultural intensification and increasing urbanisation (Corbet et al. 1991, Westrich 1996, Kremen and Ricketts 2000, Roubik 2000, Pauw 2007). The landscape structure of the UK, in common with much of western Europe, has dramatically changed: 'natural' habitat has become fragmented within a typical farmland environment that is now dominated by large agricultural fields, demarcated by narrow, interconnected field boundaries such as hedgerows and drainage ditches (Burel 1996).

Habitat fragmentation can increase the likelihood of extinction of isolated plant and animal populations due to reduced gene flow and inbreeding depression (Fahrig and Merriam 1994, Young et al. 1996, 2000, Dudash and Fenster 2000, Eisto et al. 2000, Kéry et al. 2000) and due to a greater susceptibility to environmental perturbations and other stochastic processes. Linkages within pollination webs can be particularly susceptible to reductions in habitat patch size and increased distances between habitat fragments (Rathcke and Jules 1993, Kearns et al. 1998,

Krauss et al. 2003, Steffan-Dewenter 2003, Steffan-Dewenter et al. 2006, Pauw 2007). This can lead to reduced plant population viability as pollinators determine both the quantity and quality of offspring through pollen limitation and the extent of self-fertilisation (Waser et al. 1996). Most pollinators require a spatio-temporally reliable supply of nectar (Corbet 1995) and the distance between plant populations should not exceed natural pollinator foraging distances if they are to receive sufficient pollinator service and gene flow (Kwak et al. 1996). Landscape structure is therefore important when considering the conservation of plant–pollinator interactions (Townsend and Levey 2005, Steffan-Dewenter et al. 2006, Van Geert et al. 2010).

The importance of linear landscape features such as hedgerows within the lowland arable landscape has long been recognised (Forman and Baudry 1984, Clements and Tofts 1992, Burel 1996, Davies and Pullin 2007). Not only do hedgerows provide habitat and resources for plant and animal populations (Pollard and Holland 2006, Hannon and Sisk 2009, Jacobs et al. 2009) and modify local microclimate (Sanchez et al. 2010), but they can connect otherwise isolated habitat patches, facilitating the dispersal of individuals and thus ameliorating the effects of habitat fragmentation (Baudry and Merriam 1988, Burel 1989,

Merriam 1991). Non-cultivated linear landscape features within intensively managed agricultural landscapes are therefore important as they are frequently the only connection between the remaining fragments of once extensive semi-natural habitat (Burel 1996, Baudry and Bunce 2001).

As well as acting as habitat corridors, linear landscape features may provide visual cues and act as navigational aids for highly mobile species (Rosenberg et al. 1997). However there have been few studies of insect flight behaviour in response to linear landscape features due to the difficulties of tracking relatively small organisms at large spatial scales (though see Osborne et al. 1999, Dover and Fry 2001, Cant et al. 2005, Townsend and Levey 2005). Animal movement along linear landscape features has previously been explained as the linear feature representing an extension of an organism's habitat (Rosenberg et al. 1997, Schmucki and de Blois 2009, Van Geert et al. 2010). However the architecture of linear features can facilitate movement, beyond their use by animals as resource-containing habitat. For example, Dover and Fry (2001) experimentally simulated some of the visual and physical components of hedgerows using artificial materials. They reported that butterfly behaviour was strongly affected by such artificial constructions and could educe oriented movements along the length of the linear feature. However we know little about how pollinators respond to natural linear features in a landscape and the implications of this for pollination success of plant populations (Cant et al. 2005, Townsend and Levey 2005).

To address this gap in our knowledge we carried out observations and performed experiments using artificially constructed and natural linear landscape features. We show that hedgerows facilitate bumblebee (*Bombus* spp. Hymenoptera: Apidae) movements across agricultural landscapes by changing their flight behaviour. Using a landscape-scale bioassay we also demonstrate that the spatial arrangement of linear features can influence bumblebee visits to patches of plants and the subsequent fecundity of those plants.

Material and methods

All observations and experiments were conducted at Purston Manor Estate, Great Purston, Brackley, Northamptonshire, UK (OS Landranger Map 151, grid reference: 518395). This estate is situated in a rural setting approximately 8 km from the nearest town and is representative of the landscape in lowland England (Fig. 1). It is a mixed farm of 209 ha, two thirds of which are arable and one third permanent pasture for sheep and cattle. There are few woodland areas and the undulating topography has a maximum height of 122 m a.s.l.

Bumblebee flight observations along hedgerows (a)

Observations were conducted along eight randomly selected hedgerows for 4–6 days each in June 2000. These hedgerows were separated by at least 200 m and can be considered independent replicates (Fig. 1). All of the hedgerows were set into a matrix containing low plant diversity and limited floral resources as they were adjacent to pasture or silage grassland, wheat fields or lanes. This should reduce the influence of landscape context on bumblebee flight behaviour.

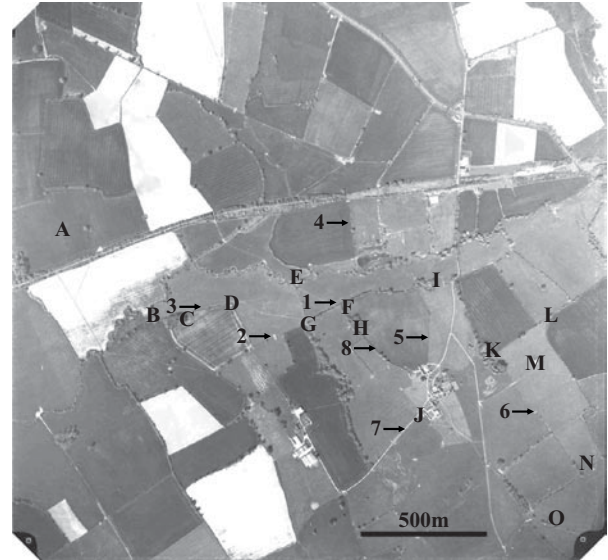


Figure 1. Aerial photograph of the Purston Manor Estate, Northamptonshire, UK, showing the positions of the eight hedgerows used to observe bumblebee flight (numbered arrows) and the positions of the 15 experimental *Salvia* patches (capital letters). Photograph taken May 1990; reproduced by permission of NRSC Ltd.

Thirty metre transects were marked out perpendicular to the axis of each hedgerow and 15 min randomised observation periods conducted at 0, 10, 20 and 30 m from the hedgerow. At each observation point we recorded the non-foraging flight behaviour of bumblebees, categorising the flight direction of each individual as linear, perpendicular, diagonal or irregular in relation to the orientation of the hedgerow (Fig. 2). Data were analysed using a univariate general linear model with number of *Bombus* individuals as the dependent factor and hedgerow identity, distance from hedgerow and flight orientation as independent factors.

Bumblebee flight observations along an experimental medium-scale array (b)

Bumblebee movements were observed to and from three patches of flowering *Phacelia tanacetifolia* (Hydrophyllaceae) a non-native species known to attract large numbers of bumblebees. Patches were equidistantly placed 30 m apart in an open, recently cut 7 ha field. Each patch consisted of six 25-cm diameter pots, with one central pot surrounded by the other five. Flower density of each patch was monitored throughout the investigation by counting the number of flowering cymes per patch each day. Each patch contained a mean (\pm SD) of approximately 40 flowering stems (patch one: 42.2 ± 4.2 ; patch two: 40.0 ± 3.8 and patch three 40.6 ± 3.7). An artificial linear feature was constructed consisting of black weed control fabric supported by poles to a height of 1.2 m, creating a triangular cross-section with a maximum width of 1.5 m at the base. This initially linked two of the *Phacelia* patches and each patch was observed for one hour per day on 16 days in July and August 2000. Following this, the artificial linear feature was repositioned to link another pair of patches and the three patches again

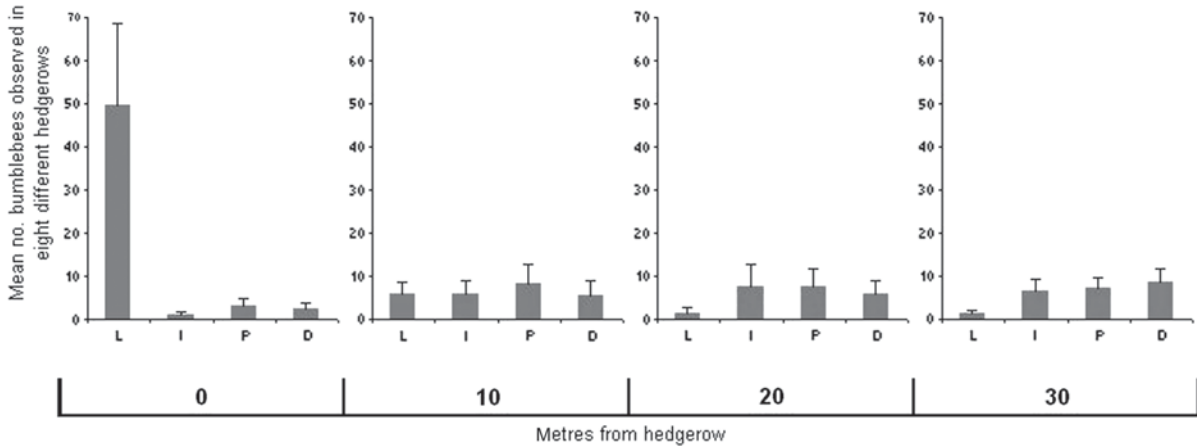


Figure 2. Observations of bumblebee of flight direction in relation to perpendicular distance from a hedgerow. Flight categories: L = linear, I = irregular, P = perpendicular, D = diagonal. A total of 1029 *Bombus* individuals were observed of at least three species. Data are means of between four and six observations per distance from each of eight different hedgerows. Error bars indicate 95% CI. Overall univariate GLM: $F = 24.5$, $DF = 9$, $p < 0.01$. The independent factors of hedgerow identity, distance from hedge and orientation were all statistically significant at $p < 0.01$. Of the interacting factors, only distance \times flight orientation was statistically significant ($p < 0.01$).

observed for a further eight days in August 2000. Bee behaviour and visitation rates can naturally vary due to differences in weather and time of day. To minimise these effects all observations took place between 11:00 and 15:00 during periods of warm, still weather and the order in which each patch was observed was randomised on each day.

All visiting bumblebees were captured and marked using queen honeybee marking discs following Kwak (1987). The identity and flight direction of individual bumblebees arriving at and departing from each patch was recorded during each observation period.

The categorical data (proportions of inter-patch movements) were analysed using G tests. The data on number of bees per patch were analysed using one way ANOVA.

Bumblebee flight observations along an experimental landscape-scale array (c)

In July 2001 we used an existing hedgerow, 180 m in length, as a connecting linear feature for patches of *Phacelia tanacetifolia*. Each patch contained 12 pots which were again monitored to standardise the number of flowering stems. Patches A and B were located at either end of a hedgerow; the third patch, C, was situated in an area of non-cultivated land surrounding a disused barn at a distance of 130 m from each of the patches A and B. This barn area was located in a wheat field and was isolated from any hedgerows. Observations of bees followed the format for the previous experiment. Data were analysed as for experiment (b) above.

Pollinator visitation bioassay experiment (d)

In July 2001 fifteen semi-natural habitat patches were identified within the estate landscape (Fig. 1). Each patch was connected to the other patches by between zero and five hedgerows, as follows: zero connections (patches 13 to 15); two connections (patches 9 to 12); three connections (patches 5 to 8); four connections (patches 2 to 4); and five connections (patch 1). Note that it was impossible to find

patches with only a single hedgerow connection them (i.e. a hedge terminating with a habitat patch) and only one patch could be located which had five connections.

Three individual *Salvia pratensis* (Lamiaceae) plants were planted directly into the ground in each patch to form a 30 cm equilateral triangle. Individual flowers on every plant were tagged and their progress monitored over 25 days. The number of seeds produced per flower was recorded as the flowers faded. There was no significant difference in mean number of flowers per patch (one-way ANOVA, $F_{14,30} = 0.77$, $p = 0.70$). Each patch was observed for insect visitors to the *S. pratensis* plants for three non-consecutive hours over 14 days. Once again, the observations were randomised with respect to patch.

Fallen flowers were collected from each plant and preserved in 70% alcohol. The stigmas were removed from the flowers and the number of pollen grains adhering to each stigma was counted using a dissecting microscope. Because the pollen grains were counted on abscised flowers, all of the viable pollen that landed on the stigma would be held in place by the germinating pollen tubes.

Salvia pratensis is self compatible but requires bumblebee visitation to set seed (Van Treuren et al. 1993, Kwak et al. 1996). The plant had previously been recorded as an extinct species from the county in which the investigation took place (Gent and Wilson 1995, McCollin et al. 2000) and consequently there were no other populations in the vicinity from which pollen may have been received.

Data were analysed using Pearson product moment correlations.

Results

Bumblebee flight observations along hedgerows (a)

Bumblebees (*Bombus* spp.) are extremely difficult to identify to species level whilst they are in flight and capturing them would have negated the point of the study. However we were able to categorise some (but not all) of the observed

individuals into broad species groups during the observation periods. The most commonly observed identifiable bumblebee taxon was the *B. terrestris/lucorum* group but the following results seem to apply to all the *Bombus* groups (Table 1). Bumblebee flight was far more likely to be linear and parallel to a hedgerow adjacent to the hedgerow than at increasing distances from it (Table 1, Fig. 2). Irregular, perpendicular or diagonal flight directions were more likely to be observed as the distance away from the hedgerow increased, and the abundance of bees also declined (Table 1, Fig. 2).

Bumblebee flight observations along an experimental medium-scale array (b)

The observation that bumblebees were more likely to fly along hedgerows rather than in adjacent open land was experimentally confirmed with the medium-scale experimental array of flower patches using an artificial linear feature. Patches of *Phacelia tanacetifolia* which were connected by the artificial linear feature were visited as often as the unconnected patch (mean number of visits per observation period - one way ANOVA: $F_{2,45} = 1.7$, $p = 0.19$). However the artificial linear feature was used by bumblebees both to approach and depart the connected patches more frequently than the isolated patch and they flew more frequently from and to the connected patches (Fig. 3a). Altering the position of the linear feature to link two different patches confirmed that it was the linkage between the patches that affected flight behaviour rather than any inherent differences in the attractiveness of the patches themselves, or their location within the landscape (Fig. 3b). During this time the connected patches were also visited more frequently than the isolated patch (mean number of visits per observation period - one way ANOVA: $F_{2,21} = 14.0$, $p < 0.01$).

Bumblebee flight observations along an experimental landscape-scale array (c)

The results of this experiment further confirmed our findings at a larger scale: the presence of the hedgerow positively affected bumblebee approaches and departures to the connected patches of *Phacelia tanacetifolia* (Fig. 3c). Due to the distances involved, it was not possible to observe direct bumblebee movement between the connected patches. However, until out of sight, bumblebees were significantly more likely to arrive to and depart from the connected patches via the hedgerow than in any other direction (Fig. 3c). Visitation rates to the isolated patch were significantly lower than those

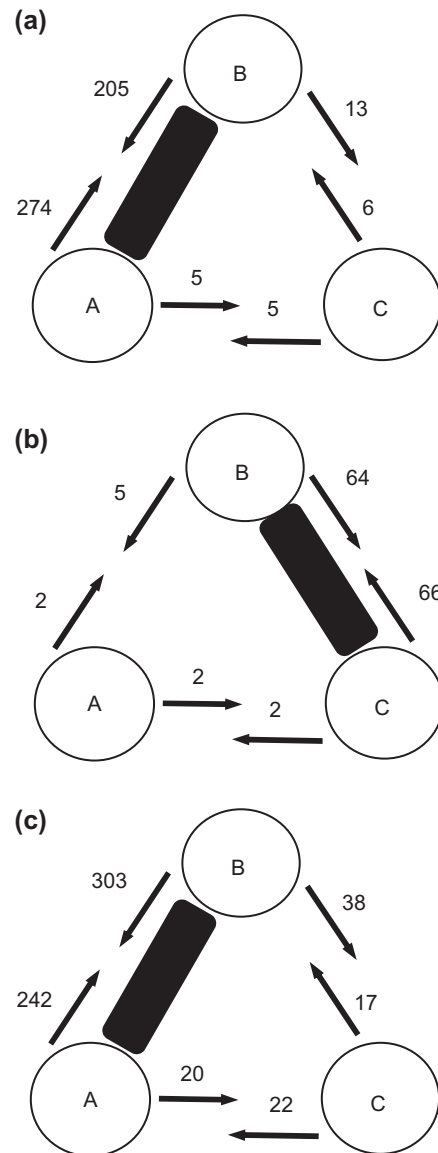


Figure 3. The number of observed bumblebee flights between patches (A, B and C) of *Phacelia tanacetifolia* in arrays connected by artificial linear features (a, b) and a natural, existing hedgerow (c), indicated by the black oblong. Statistical analyses of these data: (a) artificial linear feature before position change, proportion of inter-patch movements - G-test: $G_6 = 40.0$, $p < 0.01$. (b) Artificial linear feature after position change, proportion of inter-patch movements - G-test: $G_6 = 13.0$, $p < 0.05$. (c) Existing 180 m hedgerow, proportion of inter-patch movements - G-test: $G_6 = 106.8$, $p < 0.01$.

Table 1. Observations of flight direction relative to hedgerow orientation by different bumblebee (*Bombus*) species groups.

<i>Bombus</i> group:	Flight direction relative to hedgerow:				Total
	Linear	Irregular	Perpendicular	Diagonal	
Unidentified <i>Bombus</i> spp.	309	150	186	170	815
<i>B. terrestris/lucorum</i> agg.	144	13	18	11	186
<i>B. lapidarius/ruderarius</i>	8	3	3	2	16
<i>B. pascuorum</i>	7	2	3	0	12

to the two connected patches (mean number of visits per observation period - one way ANOVA: $F_{2,33} = 4.3$, $p = 0.02$). Furthermore, the marked bees observed visiting the isolated patch were largely comprised of a different set of bees from the ones visiting the connected patches, whereas over 90% of bees marked on patches A and B were re-observed on the connected patches. Although this experiment was conducted only once and is therefore unreplicated, it nonetheless backs up the results of the previous experiment conducted at a smaller scale and serves as an illustration of what may be occurring at a larger, landscape scale along real hedgerows.

Pollinator visitation bioassay experiment (d)

Bumblebee and hoverfly (Diptera: Syrphidae) abundance on *Salvia pratensis* plants increased as the number of connections per patch increased (Fig. 4a). There was also a significant correlation between the total numbers of legitimate pollinators (*Bombus pascuorum* and *B. hortorum*) and patch connectedness (Pearson correlation: $r = 0.68$, $DF = 13$, $p < 0.01$).

More pollen grains were deposited on the stigmas of *S. pratensis* flowers within the highly connected habitat patches (Fig. 4b) resulting in significantly higher seed-set for those plants in patches with a greater number of connections (Fig. 4c) and there was a strong, positive correlation between mean number of pollen grains per stigma and mean seed set per plant across the 15 patches (Pearson's correlation $r = 0.80$, $n = 15$, $p < 0.001$). The result was that in general,

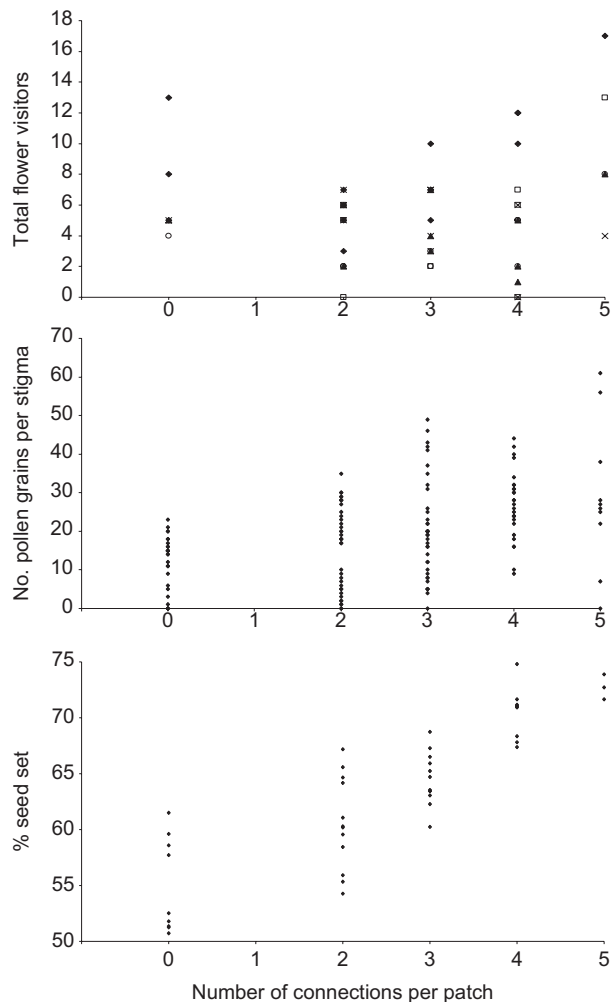


Figure 4. Results of the landscape scale bioassay using patches of *Salvia pratensis* planted into sites with different levels of hedgerow connectivity. (a) Total number of observed individual bumblebee and syrphid fly visitors per *S. pratensis* patch during 42 h of observation per patch over three days. Key: \blacklozenge *Bombus pascuorum* (Apidae); \square *B. hortorum*; \blacktriangle *B. pratorum*; \times *Episyrphus balteatus* (Syrphidae); \circ *Rhingia campestris*. Pearson correlation: $r = 0.63$, $DF = 13$, $p < 0.05$. (b) Number of pollen grains per stigma per *S. pratensis* patch. Pearson correlation: $r = 0.44$, $DF = 138$, $p < 0.01$. (c) Percentage seed-set per *S. pratensis* patch and patch connectedness. Pearson correlation: $r = 0.89$, $DF = 13$, $p < 0.01$.

plants with four or five connections produced between 7–23% more seeds than those plants within unconnected patches (Fig. 4c).

Discussion

The results from our observations and experiments have shown that hedgerows (and possibly other linear landscape features) facilitate movement of *Bombus* spp. around a typical landscape of lowland Britain. This movement is independent of foraging movements on flowers in the hedgerows and is related to the physical structure or contrast of the hedgerow in relation to the surrounding habitat, because the bees also responded to an artificial linear feature. Why do bumblebees follow hedgerows? Navigation and location of forage patches by reference to landmarks has been previously demonstrated in bumblebees (Chittka and Geiger 1995, Chittka et al. 1995, Goulson and Stout 2001, Menzel et al. 1998) and distance estimation in honeybees relies on the retinal image flow of the landscape structure and specific familiar landmarks as the bees fly along (Esch et al. 2001). Small-scale investigations with honeybees *Apis mellifera* have demonstrated that they are innately capable of relatively sophisticated visual cue assimilation and processing and will follow contours contained within black and white patterns (Lehrer et al. 1985). In relation to this, the results from our study suggest that this same pattern of landmark recognition is occurring in bumblebees at the larger, landscape scale with hedgerows being used as visual markers within the habitat matrix.

As an alternative explanation, bumblebees might conceivably follow hedgerows because their physical structure could provide shelter and afford protection from predators. However this is unlikely for a number of reasons. Bumblebees are able to fly during periods of inclement weather and can compensate for wind drift (Osborne et al. 1999, Riley et al. 1999). Also, although an insect might be more conspicuous flying over open fields, the hedgerow and its associated faunal community arguably harbours more predators and parasites than would be found in the open (Andrews 1993, Hinsley and Bellamy 2000, Fuller et al. 2001). Although it is also possible that the pattern we observed is caused by bumblebees avoiding crossing hedgerows (or their artificial analogues) we cannot conceive of a reason why this may occur.

Pollinator visitation rates, pollen deposition and seed-set were all significantly greater on *Salvia pratensis* plants in those patches with high hedgerow connectedness. It is unlikely that the positive correlation of seed-set and connectedness could have occurred merely as a result of greater densities of legitimate pollinators naturally present in the locality as bumblebees can easily travel distances across a landscape greater than the scale of the experiment (Fig. 1). Our bioassay species, *S. pratensis*, is wholly dependent on bumblebee visits to set seed (Van Treuren et al. 1993, Kwak et al. 1996) and so the greater reproductive success found in the highly connected patches was directly attributable to the higher bumblebee visitation rates recorded. We know from the previous observations and experiments that *Bombus* spp. follow hedgerows and this is the first documented example of pollinator flight directionality being strongly influenced

by landscape structure, and in turn directly affecting plant reproductive success.

In the light of the documented declines of pollinator diversity (Williams 1986, O'Toole 1993, Westrich 1996, Potts et al. 2010) and widespread habitat fragmentation in the temperate and tropical zones, understanding the effect of landscape structure on pollinator diversity and movement has never been more important (Stefan-Dewenter et al. 2006). The conservation of plant–pollinator interaction webs is far more likely to be effective at habitat or landscape levels where a wider view of the influences on plant–pollinator interactions can be taken (Corbet 1997). Pollen delivery is often the most important limiting factor on flowering plant fecundity due to the wide variation and unpredictability of spatial and temporal abundance of pollinators (Jennersten 1988, Larson et al. 1999, Knight et al. 2005). In relation to the conservation of plant populations and their pollinating animals, Townsend and Levey (2005) showed that 150×25 m habitat corridors were used by butterflies, bees and wasps to move between habitat patches, and that these insects transferred significantly more pollen compared to pollinators in unconnected habitat patches. However, our findings suggest that habitat patches or local nature reserves need not necessarily be connected with corridors of contiguous habitat in order to preserve plant population gene flow between those patches. Linear landscape features such as hedgerows and ditches would suffice to allow pollen movement, at least for bumblebee pollinated species, but possibly plants with other pollination systems; for example we know that butterflies also follow hedgerows (Cranmer 2004). However we also recognise that hedgerows could potentially isolate unconnected plant populations if hedgerows act as a 'drift fence' (sensu Haddad and Baum 1999) to channel pollinators away from isolated populations and we recommend further research at a landscape level to investigate this effect. Ultimately, maintaining hedgerows in a landscape may be an acceptable compromise in parts of the world where large scale habitat creation would interfere with agricultural activities, but where isolated populations of plants are at risk from inbreeding depression or local reproductive failure.

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