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Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape

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ABSTRACT

In Europe, oilseed rape is the principal crop used in the production of edible and renewable fuel oil products. Insect pollinators, in particular bees, have been shown to have a positive effect on the seed set of this crop. We undertook experiments looking at behavioural differences between honeybees, bumblebees and solitary bees visiting oilseed rape flowers, and related this to landscape scale responses in visitation rates. We found that behavioural differences between honeybees, bumblebees and solitary bees alter the likelihood of pollen transfer from their bodies to the plant stigma. Solitary bees and bumblebees tend to have greater rates of stigmal contact than honeybees. The interactions between the likelihood of free pollen on bodies and the probability of stigmal contact suggest that only 34.0% of visitations by honeybees were likely to result in pollen transfer to the stigma, relative to 35.1% for the bumblebees and 71.3% for solitary bees. Visitation rates were higher for honeybees in high quality landscapes with relatively large areas of alternative foraging habitat. Visitation rates of honeybees were also more frequent in the vicinity of managed hives. For solitary bees and bumblebees visitation rates did not respond to landscape structure, although more species of solitary bees were found in landscapes with a high cover of semi-natural grassland. While honeybees may be less efficient in pollen transfer per unit visit, where they numerically outweigh other types of bees in a crop (e.g. around managed hives) this may not be important. For this reason the relative ease with which hives can be moved across landscape means that honeybees are perhaps the most suitable taxa for use as a pro-active mitigation measure against pollinator deficits. However, the greater efficiency of solitary bees compensates for the effort required to implement longer term management (i.e. the establishment of flower rich field margins and open soil nesting sites) to support their populations.

1. Introduction

In Europe, oilseed rape (*Brassica napus* L.: Brasicaceae) is the principal crop used in the production of refined edible and renewable fuel oils (Wittkop et al., 2009). In the UK, it is grown on 15.8% of available arable land producing 2.8 million tonnes of seed (Defra, 2012). Areas currently cropped by oilseed rape are likely to continue to increase should current trends in both the demand and price of this crop rise (Wittkop et al., 2009; Defra, 2012). While yield increases have been seen over the last ten years (currently at 3.9 tonnes hectare^{-1}) this has principally been achieved through improved line varieties and effective agronomy (Defra, 2012). One potential mechanism to further increase yield is to promote improved pollination by insects (Hayter and Cresswell, 2006; Bommarco et al., 2012; Jauker et al., 2012). Although oilseed rape is predominantly wind pollinated (Chifflet et al., 2011), the role of domesticated and wild insect pollinators in promoting pollination is potentially economically significant (Breeze et al., 2011; Chifflet et al., 2011; Bommarco et al., 2012; Jauker et al., 2012; Ollerton et al., 2012). For example, increased insect pollination rates have been shown to raise oilseed rape yields, reduced chlorophyll content and positively impact on oil content and seed weight (Bommarco et al., 2012). However, different breeding lines and cultivars may respond differently to insect pollinators. This was shown by Steffan-Dewenter (2003) who demonstrated that high densities of pollinators could increase mean seed weight per plant for

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male sterile lines, but not male fertile lines. While insect pollinators may increase oilseed rape yields, wide-scale population declines in Europe and other parts of the world have limited their contribution to this process (Potts et al., 2010).

Considerable debate has arisen as to the roles played by different pollinator taxonomic groups in improving crop yields (e.g. Breeze et al., 2011; Aebi et al., 2012; Ollerton et al., 2012). In particular, the relative role played by actively 'farmed' domesticated honeybees (*Apis mellifera* L.: Apoidea) that are bred and moved around landscapes in artificial hives, and wild bees that are manipulated indirectly through management to improve nesting and foraging resource (Steffan-Dewenter et al., 2002; Pywell et al., 2005; Öckinger and Smith, 2007; Breeze et al., 2011; Aebi et al., 2012; Ollerton et al., 2012). Increasing global food requirements linked with the high economic value of pollination (estimated to be as high as €135 billion worldwide (Potts et al., 2010)) mean that elucidation of roles played by different pollinator taxa is crucial. This is in part because management that benefits different pollinator taxa will not necessarily be identical (e.g. Steffan-Dewenter et al., 2002; Jauker et al., 2009). For example, many solitary bees depend on the availability of bare ground as a nesting habitat (Potts et al., 2005), something that is of little importance to honeybees located in artificial hives. Independent of the relative importance of different taxa, the delivery of crop pollination services is likely to be greatest where diverse pollinator assemblages exist (Hoehn et al., 2008; Breeze et al., 2011; Ollerton et al., 2012).

Visitation rates are typically a reflection of the local density of individual pollinator species, and are likely to be an important indicator of the effectiveness of bees in promoting increased crop yields (Richards et al., 2009; Garibaldi et al., 2011). This follows on from the assumption that the more flowers visited by an individual bee so the greater the likelihood of pollen transfer (Vazquez et al., 2005; Richards et al., 2009). Certainly, the ability to manipulate visitation rate in honeybees, by directly moving hives to the location of flowering crops, gives them the greatest appeal from a crop management perspective (Breeze et al., 2011). While visitation rates of honeybees are likely to be greater than that seen for wild pollinators in the vicinity of hives, Garibaldi et al. (2011) suggests that honeybees tend to represent less than 25% of all visitations to crops. However, visitation rates alone will not represent the whole picture, as the effectiveness of bees in pollinating crops will depend on species specific behaviour on arriving at a flower (Wallace et al., 2002). Specifically, the likelihood that individuals will have pollen accessible on their body (i.e. not stored only in a pollen basket), and that this pollen then comes in contact with the stigmas of the plant, will influence pollination success (Bosch and Blas, 1994; Wallace et al., 2002). It is the interaction between visitation rates and the likelihood of con-specific pollen transfer to the stigma that will influence overall pollination success within crops. Note, we are not suggesting that these are the only limiting factors to pollination success, rather that they represent an important base line to the likelihood of pollen transfer.

In this study we look at how differences in small scale behaviour between honeybees, bumblebees and solitary bees (*Andrena*, *Osmia* and *Lassioglossum* spp.; Apoidea) affects the likelihood of pollen transfer for oilseed rape, and then relate this to landscape scale patterns in both visitation rates and species richness. We predict that: (1) the probability of pollen transfer will be lower per unit visit for honeybees than wild bees as a result of behavioural differences in how they interact with flowers (Bosch and Blas, 1994; Wallace et al., 2002); (2) visitation rates of bees will be higher at field edges than interior as bees spill-over from semi-natural habitats; (3) the impacts of landscape structure (alternative foraging and nesting habitats) will be more pronounced for bumblebees and solitary bees, as their populations are more likely to have reached an equilibrium with local conditions. In contrast, the yearly relocation of honeybee hives by professional apiarists will result in less pronounced responses to landscape structure.

2. Methods

We undertook three complementary experiments to identify links between small scale behavioural differences in honeybees, bumblebees and solitary bees in how they visit oilseed rape flowers, and their responses to landscape structure in terms of visitation rates and overall species richness. All studies were undertaken in Wiltshire, UK and focused specifically on bees (Apoidea).

2.1. Small scale taxonomic differences in behaviour

Three fields of oilseed rape (DK Cabernet variety) were selected on each of two farms in Wiltshire, UK. These were Windwhistle Farm (Lat. N51:03:12; Long. W1:53:30) and Burcombe Manor (Lat. N51:04:42; Long. W1:54:06). Individual farms were separated by *c.* 2.3 km, with fields within a farm separated by at least 300 m. For each of the six fields, two separate 50 m × 2 m fixed transects were established running into the fields from the edge along tram lines (the tyre tracks through crops resulting from farm machinery). Each transect was started at a distance of 25 m from the crop margin, with paired transects within individual fields separated by 22 m (the width of the tram lines). For two month (29/4/2012 to 31/5/2012) covering the flowering period of oilseed rape, individual transect were surveyed for bees on eight separate occasions following standard limits for weather conditions for butterfly surveys given by Pollard and Yates (1993). As the sampling season was relatively early transects were walked between 10.30 and 16.00 hours to ensure high levels of bee activity. Each transect was walked for a period of 30 min, so that a single field (the experimental unit) received 8 h of observations on a 100 × 2 m area (equivalent to 2.4 min m^{-2}).

Pollinators were identified to the following taxonomic resolution. Honeybee (*A. mellifera*); Bumblebees to species *Bombus lapidarius*, *Bombus terrestris*, *Bombus lucorum*, *Bombus pascuorum*, *Bombus pratroum*, *Bombus hortorum*, *Bombus hypnoroum*, *Bombus vestalis*, *Bombus rupestris.* Bumblebees were further distinguished between foraging queens and workers as these were both observed in large numbers; Solitary bees, identified to body forms typical of common oilseed rape pollinators. These were *Lasiglossum* spp. (genus level only), *Osmia* (separated to *bicolour* and *rufa*) and *Andrena* (separated to body forms typical of *dorsata*, *carantonica*, *nigroaenea*, *haemorrhoa*, *fulva*, *flavipies*, *nitida*, *cineraria*, *bicolour* and *minuta*). Previous non-quantitative surveys (*unpublished data*) suggest that these are the principal species that locally pollinate oilseed rape in southern Britain. As we were observing behaviour it was often not possible to take specimens and so some cryptic species may have been recorded under these 'body form' species categories. Note, this 'body form' approach is widely used for bumblebees for field observations (Edwards and Jenner, 2005). After observing a bee during transect walks the following behavioural observations were made: (1) time spent on flower head in seconds (to provide a measure of mean visitation time for each pollinator); (2) the presence of free dry pollen anywhere on the individual; (3) whether stigma contact with the oilseed rape flower is made; (4) whether the pollinator probes for nectar; (5) whether pollen is actively collected and transferred to pollen baskets. Each bee individual was observed for three separate flower visitations to obtain an average time spent on a flower, or the probability of a particular behaviour occurring. Note, if observed bees left transects before all three observations could be made this record was excluded from subsequent analysis.