Title
Bumble bee pollen use and preference across spatial scales in human-altered landscapes

Permalink
https://escholarship.org/uc/item/60n1m6nk

Journal
Ecological Entomology, 38(6)

ISSN
0307-6946

Authors
JHA, SHALENE
STEFANOVICH, LEV
KREMEN, CLAIRE

Publication Date
2013-12-01

DOI
10.1111/een.12056

Peer reviewed
Bumble bee pollen use and preference across spatial scales in human-altered landscapes

SHALENE JHA, LEV STEFANOVICH and CLAIRE KREMEN

Abstract. 1. While the discussion of native pollinator decline has grown dramatically worldwide, information on how native pollinators utilise floral resources in natural and human-altered landscapes remains relatively limited. Specifically, little is known about the collection of pollen, an essential component of larval and adult bee food, and whether pollen collection patterns change across habitats, spatial scales, and/or native and non-native floral resource distributions.

2. In this study, the pollen collection patterns and preferences of the yellow-faced bumble bee, Bombus vosnesenskii, were examined across a gradient of natural and human-altered sites.

3. Three hypotheses were investigated: (i) landscape-scale (2 km) but not local-scale (250 m) floral and habitat composition factors are most predictive of bee-collected pollen composition; (ii) collection of native pollen is greater in sites with greater proportions of natural habitat at landscape scales; and (iii) bees exhibit greater ‘preference’ for native versus non-native pollen.

4. Bombus vosnesenskii collected more species of pollen when landscape-scale riparian forest cover was low but local- and landscape-scale floral species richness was high. Also, B. vosnesenskii collected pollen from a wide range of plant families and did not exhibit a significant preference for native versus non-native species.

5. Finally, preference analysis indicated that the only significant preference exhibited by B. vosnesenskii during the study period was for Heteromeles arbutifolia, a native shrub. Overall, results from this study reveal the importance of species-rich floral patches (native and non-native) for pollinator provisioning across natural and human-altered landscapes.

Key words. agriculture, ecosystem service, foraging behaviour, pollinator, resource dynamics.

Introduction

Pollination is a critical part of wild and cultivated plant reproduction and an invaluable ecosystem service in both natural and human-altered landscapes. Animal pollination, which is provided by both wild and managed pollinators, is valued at approximately US$200 billion worldwide (Gallai et al., 2009) and contributes to the stability of food prices, food security, food diversity, and human nutrition (Steffan-Dewenter et al., 2005; Eilers et al., 2011). The urgent need to conserve native (wild) pollinators that provide crop pollination services has been exacerbated by recent catastrophic declines in managed honey bee populations (e.g. Neumann & Carreck, 2010), which illustrate that sole reliance on honey bees for crop pollination is risky. Further, recent work has shown that crop yields respond positively and far more consistently to wild pollinator richness and visitation than to honey bee visitation across many crop types, biomes, and continents (Garibaldi et al., 2013). Although native pollinators are critical ecosystem service providers, their populations currently face many threats, most often associated with habitat destruction, resulting in the loss of nesting and foraging resources (Kearns et al., 1998; Biesmeijer et al., 2006; Winfree et al., 2009).
A number of studies have investigated the local- and landscape-scale factors influencing pollinator visitation of flowers in human-altered landscapes; however, much less is known about pollen collection patterns. For bees, one of the most important pollinator groups globally (e.g. Roubik, 1995), successfully obtaining pollen and nectar is an essential step in sustaining foraging adults and provisioning the brood (Michener, 2000). Because pollen is the primary food source for bee larvae, and can vary considerably in nutritive quality between species, and can serve as a proxy for pollen usage, as flower visitors often focus on nectar collection and thus neither actively nor transfer pollen (Herrera, 1987; Alarcon, 2010). Past studies have revealed that, for various insect species, habitat composition and floral abundance influence floral visitation patterns (e.g. Steffan-Dewenter et al., 2002; Kremen et al., 2004; Jha & Vandermeer, 2010), foraging distance and scale (Westphal et al., 2006; Osborne et al., 2008; Jha & Kremen, 2013a), gene flow patterns (Jha & Kremen, 2013b), and colony growth patterns (Williams & Kremen, 2007; Williams et al., 2012), yet it remains unknown how these factors, across spatial scales, influence pollen collection.

In addition, although non-native plant species are often abundant in human-altered landscapes (e.g. Williams et al., 2011; Morandin & Kremen, 2012), little is known about the collection of native versus non-native pollen by insect visitors, especially in relation to local- and landscape-scale floral and habitat composition. Some previous studies suggest that non-native plant species can disrupt native plant–pollinator interactions (Aizen et al., 2008; Bartomeus et al., 2008) or provide less attractive floral resources than native plants (e.g. Kearns et al., 1998), while others suggest that non-native plants provide important floral resources (Ghazoul, 2002; Bjerknes et al., 2007) and could even fill phenological gaps for native pollinators (Stout & Morales, 2009). Interestingly, ‘preference’ for a resource, defined as the statistical description of resource use relative to resource availability (Beyer et al., 2010), has only recently been explored for pollen and flower visitors (Harmon-Threatt, 2011; Williams et al., 2011; Davis et al., 2012; Morandin & Kremen, 2012), despite its considerable relevance to pollinator restoration.

In this study, the pollen usage and preference patterns of the western yellow-faced bumble bee, Bombus vosnesenskii, were examined across a variety of natural and human-altered landscapes and varying floral resource distributions. Bumble bees are critical native pollinators for both wild and cultivated plants (reviewed in Kremen et al., 2002; Goulson et al., 2008a) and visit a broad range of flowering plant species, and thus are essential for the maintenance of many plant communities (Memmott et al., 2004). Furthermore, bumble bees are ideal species for the study of pollen resource usage given their large colony sizes and high resource demands. Because of their sensitivity to floral resource levels (e.g. Carvell et al., 2004; Pywell et al., 2006; Williams et al., 2012) and habitat composition (e.g. Knight et al., 2009; Goulson et al., 2010; Jha & Kremen, 2013a), among other factors, bumble bees are often the first bees to be extirpated in highly intensified human-altered landscapes (Larsen et al., 2005), and a number of species have also exhibited declines across a wide range of geographic regions (Goulson et al., 2008b; Cameron et al., 2011); thus a better understanding of bumble bee pollen preference, even across single foraging trips, could be important for informing effective conservation practices.

In this study, permutation tree modelling and preference analysis were used to investigate bumble bee pollen collection patterns and preference for native versus non-native plant species across land-use types and floral resource distributions. Past research has demonstrated that bumble bee foraging distances can frequently exceed 500 m (e.g. Darvill et al., 2004; Knight et al., 2005; Jha & Kremen, 2013a). Studies have also documented higher bumble bee abundances in areas with greater natural habitat cover (Steffan-Dewenter et al., 2002; Greenleaf & Kremen, 2006), greater general flower cover (Williams et al., 2012), and greater native flower cover (Carvell et al., 2006; Pywell et al., 2006). Therefore it was predicted that pollen collected by worker bumble bees per foraging trip will respond to habitat and daily resource levels at large (i.e. landscape) spatial scales, and that pollen loads will be comprised of predominantly native plant species. Specifically, three major hypotheses were tested: (i) landscape-scale (2 km) floral resource and habitat composition are more predictive of daily bumble bee worker pollen load composition than local-scale (250 m) floral resource and habitat composition; (ii) foraging bumble bee workers collect more native pollen species per day in areas dominated by natural habitat; and (iii) bumble bees exhibit greater ‘preference’ for native versus non-native pollen.

Materials and methods

Study sites and land classification

The research area extends from Sonoma to Sacramento County in northern California and includes a wide range of human-altered and natural habitat (e.g. Kremen et al., 2002, 2004). Research was conducted from 1 June to 14 July of 2009 in eight independent study regions which varied in the proportion of human-altered habitat (cultivated crops, orchard, bare ground, and impervious areas) and natural habitat (grassland, oak woodland–chaparral, and riparian forest) within a 2 km radius (5–95% natural cover, mean = 51 ± 39%). Thus all cultivated study regions included at least 5% natural habitat, usually comprised of hedgerows or buffer strips inhabited by native plants. All study regions were separated by more than 3 km (Jha & Kremen, 2013a) (Fig. 1a).

In this study, ‘local-scale habitat composition’ is defined as land use within a 250 m radius and ‘landscape-scale habitat composition’ is defined as land use within a 2 km radius, the smallest and largest scales that have been consistently utilised for understanding land use in previous bumble bee studies (e.g. Steffan-Dewenter et al., 2002; Goulson et al., 2010). Using data from the National Agriculture Imagery Program (2009 NAIp, http://www.fsa.usda.gov/), land cover data was digitised and hand-classified within a 250 m and 2 km radius of each site.
Shalene Jha, Lev Stefanovich and Claire Kremen

Fig. 1. (a) Map of the research area: white squares, study regions; lighter colours represent natural landscapes (grassland, oak woodland–chaparral, and riparian forest); darker colours represent water bodies and human-altered landscapes (cultivated crops and urban areas). (b) A close-up of the western-most study region showing the five sampling sites separated by 300 m.

using ArcGIS®. Habitat classifications were confirmed with ground-truthing surveys at every site. Habitat was classified into seven categories: crop, grassland, orchard, bare ground, paved ground, oak woodland–chaparral, and riparian forest; however only the three natural habitat cover types, grassland, oak woodland–chaparral, and riparian forest, were considered for the analyses because these were the only land types with flowering plants.

Study species and pollen measurements

Pollen loads of Bombus vosnesenskii Radoszkowski, the yellow-faced bumble bee, were examined across the eight study regions. This is the most common bumble bee in California and one of the most important native pollinators on the west coast (Kremen et al., 2002). Like many other bumble bees, B. vosnesenskii is polylectic and nests primarily underground in large colonies of often 200–300 workers (Shelly et al., 1991). To examine the pollen collection patterns of B. vosnesenskii, an average of 20.8 (±2.18 SE) bees were net-collected in a single day across five sites located 300 m apart on a 1.2 km transect within each of the eight study regions (40 sample locations) (Fig. 1b). However, in three of these three sites no workers were carrying pollen loads, leaving a total of 37 sample sites for the study. Individual bees were temporarily immobilised and pollen loads were collected using sterilised forceps to scoop pollen from the right corbicula. The pollen load was then immediately stored in 1 ml of 95% ethanol. Given that individual bumble bees often specialise on only a few plants (Kleijn & Raemakers, 2008), pollen loads were pooled from five individuals per site to estimate B. vosnesenskii pollen usage across multiple individuals. Five individuals were selected because this was the minimum number of individuals that carried pollen loads out of all individuals collected at any given site. Specifically, when more than five individuals carried pollen loads, five B. vosnesenskii individuals per site were randomly selected. Then 10 μl from each sample was mixed for a 50 μl total pooled sample per site. The 50 μl pooled sample was then vortexed for 1 min, and 10 μl was applied to a microscope slide containing 20 μl of a glycerol and fuschin stain (Kearns & Inouye, 1993). The stain and pollen microscope slide was allowed to rest for 24 h (to allow the pollen grains to rehydrate). The first 300 pollen grains were identified to species based on a reference collection (see details below); however, Aster species could not be reliably distinguished from one another, thus these species were pooled for analyses. As per other bumble bee diet breadth studies (e.g. Goulson & Darvill, 2004), Simpson’s diversity index was calculated for each sample. To build the pollen reference collection, pollens from all flowering plant species encountered in the vegetation surveys (described below) were sampled by collecting and storing five anthers from each species in 95% ethanol. Following the staining protocol described above, the samples were mounted and used as a reference for pollen identification. More than 91% of pollen grains collected by bumble bees in this study were identified to species.

Vegetation surveys and pollen reference collection

While satellite imagery could be used for local- and landscape-scale habitat classification and quantification, vegetation surveys were required for floral species identification and quantification. Vegetation surveys were conducted on the same day as the pollen collection, and comprised of 12 randomly placed 1 × 1 m quadrats that were surveyed at every site along each transect (five patches per transect) and between sites, 300 m perpendicular to the transect (four patches per transect) for a total of 108 1 × 1 m quadrats in nine patches surveyed on each transect (i.e. per study region). Flowering species richness, number of flowering inflorescences, and petal area per inflorescence were recorded for each quadrat. Floral cover was then calculated based on inflorescence count multiplied by the petal area per inflorescence. Inflorescence counts were found to be good predictors of overall pollen availability, as documented for similar plant species within the same bioregion (Harmon- Threatt, 2011). In this study, 'local-scale
floral’ resource factors are those that were measured within each site (the mean, CV, and total species richness of the 12 vegetation quadrats within a patch), and ‘landscape-scale floral’ resource factors are those measured across all sites in the study region (the mean, CV, and total species richness among all 108 quadrats in all nine patches).

Data analysis

Role of local and landscape variables. Non-parametric regression trees were used to determine the most important factors predictive of the four pollen response variables: (i) pollen load species richness; (ii) pollen load diversity (Simpson’s diversity index); (iii) pollen load native species richness; and (iv) proportion of native pollen. Regression trees are commonly used to examine patterns in ecological data, and are especially useful for developing habitat models because they do not assume linearity in response variables and allow factors to interact in a hierarchical fashion. In this study, non-parametric regression trees are especially useful, given their ability to resolve critical values (i.e. thresholds) for relevant explanatory variables, which can then be useful for developing guidelines for specific conservation management practices (reviewed in De’ath & Fabricius, 2000). Specifically, vegetation restoration protocols can be designed by directly using the thresholds derived for each of the explanatory vegetation variables. These thresholds represent a valuable new contribution to pollinator restoration ecology, given that most current pollinator restoration practices are based on visitation rather than pollen usage data (Frankie et al., 2005; Menz et al., 2011).

Non-parametric regression trees were built utilising the ‘party’ package in R (R Development Core Team, 2013; Strobl et al., 2009). The non-parametric regression trees estimate a regression relationship by utilising a binary recursive data-partitioning algorithm. The trees function by first testing whether input variables are independent of one another and independent of the response variable. If this hypothesis is rejected, then the input variable with the greatest association to the response variable is selected, as measured by a P-value for the test of the partial null hypothesis of the single input variable and the response variable. The data are then split by the response variable into two sections (nodes) and the search for the input variable with the next greatest association to the response variable is repeated. This process continues until the criterion (0.95) does not exceed the minimum established in the analysis.

Because habitat composition was correlated across local and landscape scales, these two scales were examined in two separate sets of non-parametric regression trees. In the first set of trees, all floral resource factors were included: (1) local (within patch) floral cover, (2) local coefficient of variation (CV) of floral cover, (3) local floral species richness, (4) local CV of floral species richness, (5) landscape (among patches) floral cover, (6) landscape CV of floral cover, and (7) landscape total floral species richness. Then, for this first set of trees, only local-scale habitat composition factors were included: (8) the proportion of grassland within 250 m, (9) the proportion of oak woodland–chaparral within 250 m, and (10) the proportion of riparian forest in a 250 m radius of each site. In the second set of trees, all the floral resource factors (1–7) were included, along with the landscape-scale habitat composition factors: (8) the proportion of grassland within 2 km, (9) the proportion of oak woodland–chaparral within 2 km, and (10) the proportion of riparian forest within 2 km of each site. Site locations per study region exhibited substantial variation in floral and habitat composition at the 250 m scale, therefore the five sample sites per study region were treated as independent for the local-scale analyses. However, given the proximity of sampling sites within a study region, which could be interpreted as ‘repeated sampling’ and potentially bias tree-building (De’ath & Fabricius, 2000), the package ‘coin’ (Hothorn et al., 2008) was used to examine the significance of local-scale explanatory variables, given stratification within a study region (these P-values are reported as ‘study region-stratified’). Native plant cover and species richness was not analysed because native plant cover and species richness were significantly correlated with total plant cover and total plant species richness (Pearson correlation coefficient, $r = 0.536$, $P = 0.0006$, and $r = 0.645$, $P < 0.0001$, respectively).

Species usage and preference. Classical compositional analysis (Aebischer et al., 1993) was used to identify species selection for all species comprising more than 0.1% of the pollen load. Compositional analysis can be used to identify pollen species that are collected significantly more than expected relative to their availability (e.g. Davis et al., 2012). Compositional analysis of pollen was implemented using the ‘adehabitatHS’ package (Calenge, 2006) developed in R. In these analyses, matrices of floral species availability (proportion of floral cover) and floral species use (proportion of pollen load) per site were first transformed using log-ratio analysis, which is one of the most appropriate transformations for proportional values (Aitchison, 1982). Second, overall pollen selection was examined by testing if pollen species use is significantly non-random relative to availability per site, using a randomisation test (10 000 repetitions) and assuming Wilks’ lambda ($\lambda$). Species were also classified into non-native and native groups and overall preference for either group was tested. Finally, a preference ranking matrix was built representing the mean difference between the proportion of pollen use and proportion of floral cover for each species per site, and a randomisation test (10 000 repetitions) was used to assess the significance of preference for one species over each other species (Aebischer et al., 1993; Calenge, 2006).

Results

Role of local and landscape variables

A total of 30 plant species were found flowering within the sites (13 native and 17 non-native) and a total of 22 plant species were found in the pollen loads (eight native and 14 non-native) (Fig. 2). Native species comprised 63.4% of the
floral cover and 81.1% of pollen loads collected by bumble bees. The largest fraction of pollen loads were comprised of three native species: *Heteromeles arbutifolia* (37.8%) (Rosaceae), *Eschscholzia californica* (26.8%) (Papaveraceae), and *Acmispon glaber* (9.12%) (Fabaceae) (Fig. 2). Of the identified pollen grains, 10 different families were represented, while the vast majority of pollen (> 85%) was collected from plant species in the Rosaceae, Fabaceae, and Papaveraceae (Fig. 2b).

Pollen load species richness and pollen load diversity were not significantly explained by any floral or habitat composition variable at either the local or landscape scale (P > 0.15 for all variables). The proportion of native pollens per load was significantly higher when mean local-scale floral cover was less than 0.192 m² (P < 0.001; study region-stratified, P = 0.048; Fig. 3a). The number of native species per pollen load was significantly higher when, jointly, the proportion of landscape-scale riparian forest cover was < 0.208 (P = 0.001), local-scale species richness was > 1 (P = 0.012; study region-stratified, P = 0.049), and landscape-scale floral species richness was > 4 (P = 0.044) (Fig. 3b).

**Species usage and preference**

The randomisation test for overall species selection was not significant (λ = 0.205, P = 0.323), nor was the test for native versus non-native species (λ = 0.981, P = 0.867). However, *B. vosnesenskii* significantly selected the native species, *H. arbutifolia*, in greater amounts relative to its abundance and significantly more than every other species except the non-native species, *Lotus corniculatus* (Table 1). Despite making up large portions of bumble bee pollen loads (Table 1, Fig. 1), two native species, *E. californica* and *A. glaber*, were not significantly selected in greater proportion than their abundances.

**Discussion**

This study examined the role of plant origin (native versus non-native) and multiple scales of floral resource and habitat composition on *B. vosnesenskii* pollen collection and preference per foraging trip. While no factors were found to predict total pollen richness or diversity collected per...
Thus at the intersection of row $i$ and column $j$, a positive symbol (+) indicates that species $i$ is used more than species $j$, and a negative symbol (−) indicates otherwise. Significant differences are indicated by tripled signs. Pollen load indicates ranking according to abundance in pollen load; Floral availability indicates overall floral availability across sites, where 1 = highest rank. Native species are marked with an asterisk.

day, native pollen collection was predicted by both local-scale (within patch) and landscape-scale (among patches) floral cover and species richness. There was no support for the second hypothesis that greater natural habitat cover at the landscape scale would result in higher pollen richness. Natural habitat cover was a significant predictor for only one pollen response variable (number of native pollens per sample), but in the opposite direction to our prediction. There was also no support for the third hypothesis; while bumble bees collect more native than non-native pollen (absolutely and relative to abundance), this relationship was not significant. However, analyses indicate that *B. vosnesenskii* did exhibit a significant preference for the native rosaceous species *H. arbutifolia*.

Regression tree analyses indicate that *B. vosnesenskii* responds to floral resource levels across both local (within patch) and landscape (among patches) scales. Past studies indicate that bumble bees can forage long distances (Darvill et al., 2004; Knight et al., 2005; Hagen et al., 2011; Jha & Kremen, 2013a) and that their visitation is often related to resource availability at large spatial scales (750–3000 m; Steffan-Dewenter et al., 2002; Westphal et al., 2006, 2009). Results from this study, though gathered across a single foraging day, also support the importance of both local and landscape scales, and additionally suggest that bumble bees gather pollen from a greater number of native plant species.
when both landscape and local floral species richness is higher. Bumble bees are generalists (Memmott, 1999) and often visit several floral species for pollen and nectar within a single foraging bout (Goulson et al., 2008a). The act of collecting multiple pollen species could be advantageous to bumble bees because the nutrition content of pollen and nectar varies considerably between plant species (Gardener & Gillman, 2001; Kitaoka & Nieh, 2009) and because multiple pollen species are important for bee larval growth (Genissel et al., 2002; Tasei & Aupinel, 2008).

Habitat composition was a significant predictor of native species pollen richness per sample, although native species richness was significantly lower in landscapes with greater riparian forest cover. One potential explanation for this pattern could be greater bumble bee specialisation (collection of fewer native plant species) in landscapes with more extensive riparian forest cover. Foraging studies using experimental arrays indicate that within a foraging bout, bumble bees will continue foraging on a single species as long as rewarding conspecific flowers are available within close distance (e.g. Chittka et al., 1997), thus if greater riparian forest availability provides more consistent access to a preferred native species, a reduction in native species richness of the collected pollen may be evident. Furthermore, if riparian forest habitats provide higher resource levels than other habitat types, as documented within the study region for a different native bee species (Williams & Kremen, 2007), then B. vosnesenskii may forage ‘optimally’, by increasing diet breadth in low resource areas, and decreasing diet breadth in high resource areas (Macarthur & Pianka, 1966), such as the riparian forest habitat. Experimental work on individual pollinators has found strong support for optimal foraging (e.g. Kunin & Iwasa, 1996), especially for bumble bees (Pyke, 1975; Fontaine et al., 2008), although other studies suggest that bumble bees may actually increase foraging distance in order to visit patches with high flowering plant species richness (Jha & Kremen, 2013a).

Two previous studies have found that habitat composition alone can be predictive of pollen load composition for some bee species (Goulson et al., 2002; Williams & Kremen, 2007). In this study, while habitat was predictive of native pollen species richness, the dominant variables influencing pollen collection were related to floral composition within and across patches. Although pollen collection patterns were assessed across foraging trips, research conducted across multiple time periods within the same study system has found that floral resource availability, calculated over a landscape scale, was also strongly related to growth of experimental bumble bee colonies (Williams et al., 2012). Overall, findings from this study support the importance of floral resource availability in determining native pollen collection patterns at local and landscape scales.

Species use and preference

The three largest portions of B. vosnesenskii pollen loads were comprised of the native species H. arbutifolia, E. californica, and A. glaber (Rosaceae, Papaveraceae, and Fabaceae, respectively). Bumble bee pollen loads were not dominated by the Fabaceae, as seen in many past studies (Goulson & Darvill, 2004; Goulson et al., 2008b), but included substantial amounts of pollen from the Papaveraceae and Rosaceae (as seen in Carvell et al., 2006). While this study examined pollen loads per foraging trip, unlike these past studies, findings from this study are congruent with the findings of Carvell and colleagues in indicating an important role for plants within the Fabaceae, but an equally strong role for other plant families.

Most importantly, a significant preference for the native species H. arbutifolia was documented in this study. Heteromeles arbutifolia is common across chaparral and riparian forest systems in the tall shrub communities of California (Hanes, 1974). This species provides structural diversity to landscapes often dominated by shorter-statured vegetation and thus is believed to be important for birds and small mammals in the form of nesting resources and predation protection (McMurray, 1990). Because of its critical role in bird and mammal ecology and its rapid growth and erosion control abilities, H. arbutifolia is often used in native plant restorations in California (Magill, 1974; Lowry, 1999; Morandin et al., 2011). Findings from this study illustrate the ecological importance of H. arbutifolia as a major component of B. vosnesenskii pollen collection and thus highlight the potential overlap in species selection to restore both degraded habitats and native pollinator communities (Menz et al., 2011).

Research examining historical and contemporary bumble bee pollen collection in the UK suggests that narrow diet breadth and inability to utilise non-native species may explain the rarity of some European bumble bee species (Kleijn & Raemakers, 2008). In the study system described, pollen use was examined over a much shorter time scale and for a species that does not appear to be in decline (Cameron et al., 2011); here, a preference for non-native or native species was not documented. Rather, the utilisation of non-native or native plant species generally corresponded with abundance of those species in the community. Studies conducted within the same study region have similarly found that, while collection of non-native pollen by native bees is substantial, it is no greater than expected given the abundance of non-native plants in the community (Williams et al., 2011). Interestingly, results from this study contrast a recent study conducted on restored native plant hedgerows in the same study region, where flower-visiting bee abundance, richness, and diversity were greater on native plants compared with exotic weed species (Morandin & Kremen, 2012). These differences may occur because the current study focused on a single bee species rather than the entire bee community, and because pollen collection was measured rather than floral visitation, which assesses visits for both pollen and nectar.

Broader impacts

A critical step in pollinator conservation is determining what floral species are preferred by pollinators for nectar and pollen resources (Williams et al., 2010; Winfree, 2010). While pollinator restoration projects, like the installation of flowering hedgerows, are gaining attention across the globe (Pywell et al.,

© 2013 The Royal Entomological Society, Ecological Entomology, 38, 570–579
2005; Carvell et al., 2006; Winfree, 2010), many restoration plant species lists are based primarily on visitation records, not on pollen and nectar usage (Frankie et al., 2005; Menz et al., 2011). Results from this study indicate that B. vosnesenskii utilise pollen from a wide range of plant families, including both native and non-native species. The results also indicate that a greater proportion of native pollen is collected when local floral cover is low, such as in agricultural landscapes with monoculture plantings. This is probably due to collection on the few native plants found within the hedgerows and buffer strips, and thus suggests that native plantings within agricultural landscapes can be important food resources for native bees (e.g. Morandin & Kremen, 2012). Additionally, results from this study suggest that maintaining high-flowering plant species richness across spatial scales may allow bumble bee colonies to collect greater numbers of pollen species.

Overall, these results are congruent with restoration practices which suggest that farmers and land managers do not need to rely solely on the availability of existing natural habitat to provide pollinator resources (e.g. Pywell et al., 2006; Carvell et al., 2007; Morandin & Kremen, 2013). Farmers and land managers can coordinate the creation of multiple diverse floral resource patches across their land to provide pollinators with floral resources at both local and landscape scales.

Acknowledgements

We would like to thank Jennifer Hanson and Amber Sciligo for help in the lab and field. This work was supported in part by the National Geographic Society and the UC Presidential Postdoctoral Fellowship (to S.J.).

References


Knight, M., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J.,


Harmon-Threatt, A. (2011) Pollen preference by native bumble


Accepted 3 June 2013
First published online 23 September 2013