Spatial and taxonomic patterns of honey bee foraging: A choice test between urban and agricultural landscapes

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Abstract

The health of honey bee colonies cannot be understood apart from the landscapes in which they live. Urban and agricultural developments are two of the most dramatic and widespread forms of human land use, but their respective effects on honey bees remain poorly understood. Here, we evaluate the relative attractiveness of urban and agricultural land use to honey bees by conducting a foraging choice test. Our study was conducted in the summer and fall, capturing a key portion of the honey bee foraging season that includes both the shift from summer- to fall-blooming flora and the critical period of pre-winter food accumulation. Colonies located at an apiary on the border of urban and agricultural landscapes were allowed to forage freely, and we observed their spatial and taxonomic foraging patterns using a combination of dance language analysis and pollen identification. We found a consistent spatial bias in favor of the agricultural landscape over the urban, a pattern that was corroborated by the prevalence in pollen samples of adventitious taxa common in the agricultural landscape. The strongest bias toward the agricultural environment occurred late in the foraging season, when goldenrod became the principal floral resource. We conclude that, in our study region, the primary honey bee foraging resources are more abundant in agricultural than in urban landscapes, a pattern that is especially marked at the end of the foraging season as colonies prepare to overwinter. Urban beekeepers in this region should, therefore, consider supplemental feeding when summer-blooming flora begin to decline.

Key words: apiculture, pollinator, floral resources, urban beekeeping, dance language

Introduction

The collective ability to survey a large foraging area and concentrate foraging effort on the most rewarding resources is a hallmark of honey bee foraging biology (Seeley 1995). This ability is conferred by the sophisticated dance language (von Frisch 1967) whereby individual foragers integrate their knowledge of resource availability, scent, and location (Seeley 1995; Gruter and Farina 2009). The intelligibility of the dance language to human observers allows the logic of honey bee foraging to be inverted to yield ecological insight: as a honey bee colony assesses its environment and allocates its foragers to the most rewarding resources, the spatial allocation of foragers revealed by the dance language can be used to infer the types of available habitat most suitable for honey bee foraging (Couvillon et al. 2014a; Garbuzov et al. 2014, 2015; Couvillon and Ratnieks 2015). Spatial habitat inferences from dance language analysis can also be
supported by the taxonomic identification of pollen loads collected by honey bees in the same study area (Garbuzov and Ratnieks 2013; Garbuzov et al. 2015).

Understanding the suitability of different habitat types for honey bee foraging is of central importance in the task of improving honey bee health and productivity, and honey bee habitat utilization may also inform the conservation of other pollinator species (Hartel and Steffan-Dewenter 2014). Moreover, the foraging decisions made by a honey bee colony with respect to its surrounding landscape can furnish theoretical insights into how the honey bee foraging system has evolved to optimize the collection of resources in complex environments (e.g. Visscher and Seeley 1982).

Because of the honey bee’s close association with humans, any discussion of honey bee foraging habitat must emphasize the role of human land use in shaping the composition, distribution, and abundance of floral resources (Hartel and Steffan-Dewenter 2014). Two main categories of human land use, urban development and agricultural cultivation, are comparably profound but divergent departures from a natural or semi-natural condition, and it is important to understand their respective effects on honey bee health. Studies directly comparing urban and agricultural landscapes with respect to honey bee health are equivocal, perhaps reflecting the enormous diversity of landscape composition subsumed by the terms ‘urban’ and ‘agricultural’. In the UK, Garbuzov et al. (2014) found that honey bees located within the city of Brighton foraged almost exclusively within the urban environment rather than extending their flights into the agricultural countryside, and Donkersley et al. (2014) found that the protein content of bee bread was correlated positively with urban land use and negatively with agricultural land use. In Denmark, hives located in pre-dominantly urban landscapes were shown to have a higher average weight than those in mixed or pre-dominantly agricultural landscapes (Lecocq et al. 2015). In the Midwestern USA, however, Sponsler and Johnson (2015) found that agricultural landscapes tended to favor honey bee productivity compared with urban or semi-natural (forest) habitat. Similar results were reported from Luxembourg, where Clermont et al. (2015) found frequent positive correlations between various forms of urban land use and honey bee overwintering colony loss, while certain forms of agriculture and rural land use tended to be negatively correlated with colony loss. Other studies of honey bees in either urban or crop-dominated landscapes (not in direct comparison) have often suggested negative effects of both compared with more diversified landscapes (Steffan-Dewenter and Kuhn 2003; Couvillon et al. 2014a; Odoux et al. 2014; Requier et al. 2015; Danner et al. 2016; Dolezal et al. 2016; Smart et al. 2016; Youngsteadt et al. 2015).

Here, we directly compare the foraging quality of urban and agricultural landscapes by a field-scale choice test using honey bee colonies located at a site along the interface of city and farmland. To determine the relative allocation of foraging activity between these two landscapes, we use a combination of dance language analysis and pollen identification to infer both spatial and taxonomic patterns of foraging.

**Methods**

**Study site and timeframe**

An apiary consisting of five honey bee colonies—two in standard Langstroth hives and three in three-frame observation hives—was established on the grounds of a historic cemetery located on the western edge of the metropolitan area of Columbus, OH (Fig. 1). Using QGIS 2.1 software (QGIS Development Team 2016), we digitized the landscape within a 5-km radius of the apiary and classified it using the binary categories of ‘urban’ (predominantly residential and commercial) and ‘agricultural’ (predominantly field crop). Digitization was performed by tracing the boundaries between residential/commercial development (‘urban’) and neighboring farmland (‘agricultural’) visible in 2013 aerial imagery from the Ohio Statewide Imagery Program, corroborated by reference to the 2011 National Land Cover Database land use layer (Homer et al. 2015). While the categories of ‘urban’ and ‘agricultural’ represent internally heterogeneous landscapes, parsing these categories into more specific landscape classifications was beyond the scope of this study; our central question was how the general land use syndromes represented by the terms urban and agricultural affect honey bee foraging. Thus, roadways and small residential areas occurring in predominantly agricultural surroundings were classified as part of the larger pattern of agricultural land use, similarly, forest patches and fields occurring in pre-dominantly built-up surroundings were classified as urban.

Our study was conducted in the summer and fall of 2014, beginning in late July and continuing to late September. This time frame encompasses the phenological transition between summer and fall flora along with the critical period of pre-winter food storage.

**Dance recording and decoding**

From 7 August to 26 September 2014, dance behavior was recorded one day per week from the three observation hives, representing a total of seven days of foraging activity (no dances were recorded on August 21 due to poor weather conditions). On each recording day, a morning (0930–1100 h) and an afternoon (1300–1600 h) session were recorded, each lasting ~45 min. During each recording session, all three colonies were recorded simultaneously using three separate cameras. See Supplementary Material S1 for a description of the camera models used.

Video from each recording session was first split into 1-min segments, and then every fifth segment was subsampled for analysis. Each 1-min analysis segment was imported separately into the FIJI distribution (Schindelin et al. 2012) of the image analysis software ImageJ (Schneider et al. 2012), and dances were decoded using the MTrackJ plugin (Meijering et al. 2012). Following Couvillon et al. (2012), four waggle runs from each dance were decoded, including two right turns and two left turns. See Supplementary Material (S1) for details on the application of FIJI to dance decoding.

Decoded dances from all three colonies were mapped together using the Bayesian probabilistic method developed by Schürch et al. (2013) in which decoded locations are plotted not as discrete points, but as probability clouds derived by sampling 1000 point location estimates from the posterior probability distribution of each dance. This method acknowledges the intrinsic uncertainty in the dance language and allows for the computation of credible intervals to test for habitat-based foraging biases (Garbuzov et al. 2014, 2015).

**Pollen collection and identification**

The two Langstroth hives were fitted with bottom-mounted pollen traps (Sundance I, Ross Rounds, Inc), and pollen was collected in one-week intervals on the same schedule as the dance
recordings plus one sample on 31 July prior to the first date of dance recording. To minimize nutritional stress, pollen was alternatively trapped from only one of the two colonies each week while the other was allowed to forage freely. Thus, each pollen sample represents seven consecutive days of pollen trapping for one of the two colonies. Upon return to the laboratory, pollen samples were stored in an airtight container at -20°C.

A pollen reference collection was constructed by collecting floral specimens from the vicinity of the research apiary and from other locations in the region. ~360 voucher specimens were collected, and an additional 74 pollen samples were collected directly from the anthers of plants in curated botanical gardens. All specimens were identified to the lowest possible taxonomic level. For a complete list of voucher specimens and prepared reference slides, see Supplementary Material S3.

Trapped pollen was first weighed (wet weight) and subsampled. From samples with a total mass of >100 g, a 10 g subsample was taken. All other samples were subsampled at 10% of their total mass. Pollen pellets from each subsample were then sorted by color, texture, and other visual characteristics into preliminary taxonomic groups, with mixed pollen pellets (i.e. rarely occurring single pellets consisting of visible bands of contrasting pollens, such as described by Percival (1947)) and singletons (groups represented by only one corbicular pollen pellet) being omitted from further analysis. These preliminary taxonomic groups were weighed and then scanned using a flatbed scanner (Canon LiDE 210) to record the visual characteristics of the pollen prior to the destructive process of microscopic preparation.

From each of the preliminary groups, 10 pollen pellets (or all pellets for groups having fewer than 10 total) were mixed with several drops of water in a microcentrifuge tube to form a homogenous suspension. Then, small aliquots of suspended pollen were mounted on a microscope slide using glycerin jelly stained with basic fuchsin (Kearns and Inouye 1993).

Mounted pollen specimens were examined at ×400–1000 and identified by comparison with similarly prepared specimens from the reference collection and by the corbicular characteristics recorded in the scanned images. For slides containing >1 pollen type (due to imperfect sorting or mixed foraging), the relative abundance of each pollen type was estimated by identifying and counting all grains within the microscope field of view and shifting the field of view until a total of ~500 grains were counted. Because the grains of different pollens vary widely in size, it is more informative to express the relative abundance of different pollens in terms of volume rather than grain count (O’Rourke and Buchmann 1991). Following O’Rourke and Buchmann (1991), we modeled each pollen type as either a sphere or ellipsoid and estimated its volume by measuring its mean polar and equatorial axis length (based on five randomly selected grains) and applying the corresponding formula. The proportional volume of each pollen type was then multiplied by the total mass of the sorted group represented by the microscope slide to estimate the proportion of the total mass contributed by each pollen type.

**Statistical analysis**

Following Garbuzov et al. (2014, 2015), we computed Agresti–Coull 95% credible intervals for the proportion of urban
foraging activity, treating the apportionment of point locations between the urban and agricultural landscape classes as a binomial distribution. Pseudoreplication was avoided by dividing the number of urban points ($p$) and the total number of points ($n$) by the number of simulations of each dance (1000) (Garbuzov et al. 2014, 2015). Credible intervals not including 0.5 (i.e. an equal apportionment of urban and agricultural foraging) were interpreted as indicating a statistically significant positive or negative bias. Credible intervals were computed individually for each day of dance recording and then also for the pooled data set of all days. All analyses were performed in R (R Core Team 2015) using the ‘prevalence’ package (Devleesschauwer et al. 2014).

**Results**

**Spatial foraging patterns**

For all dates, the majority of foraging activity occurred in the agricultural landscape, and this bias was significant in each case (credible interval for proportion of urban foraging < 0.5) (Fig. 2). The proportion of urban foraging rose each sampling date from 7 August (0.16) to 4 September (0.38), began to decline on 12 September (0.20), and then fell sharply on 19 September (0.04) and remained low on 26 September (0.10).

Foraging activity was most concentrated near the apiary, as expected from previous studies of honey bee foraging distance.
(e.g. Couvillon et al. 2014b). When foraging activity ranged >1 km from the apiary, it was consistently concentrated in the agricultural landscape to the south and west, though occasional foraging occurred along the urban–agricultural interface to the north (7 August, 4 September) and in the urban landscape to the east (12 September) (Fig. 3). The most distant foraging occurred 4 September, when a small amount of activity occurred in the agricultural landscape ~4 km southwest of the apiary.

**Taxonomic foraging patterns**

Between 31 July and 12 September, pollen samples were comprised mainly of legumes (Trifolium and Chamaecrista) and wild carrot (Daucus carota) (Fig. 2). These gradually gave way to Canada goldenrod (Solidago canadensis), which became the predominant pollen source in the last two weeks of the study period. Beside these major taxa, many minor pollen types occurred in low abundance. A total of 42 pollen types were identified in our samples, representing at least 11 plant families (Supplementary Material S2), and this number almost certainly underestimates the true taxonomic richness due to our omission of singleton pollen pellets. In addition to these, one sample contained several pellets of fungal spores, as has been occasionally documented by other observers (Wingfield et al. 1989).

**Discussion**

Honey bees in our study exhibited a consistent, and often dramatic, foraging bias in favor of the agricultural over the urban landscape. This pattern, observed directly in our spatial foraging data, was corroborated taxonomically by the overwhelming prevalence in our pollen samples of flora common in Midwest agricultural landscapes (D. carota, Trifolium spp., Chamaecrista fasciculata, S. canadensis). It should be noted that spatial patterns inferred from dance analysis reflect both pollen and nectar foraging, whereas pollen identification reveals only the former. Nevertheless, most of the flora that dominated our pollen samples—particularly the Trifolium spp. and S. canadensis—are also known to be major nectar sources for honey bees (Pellet 1920; Goltz 1975; Ayers and Harman 1992), so it is likely that the spatial foraging patterns we observed largely represent patches of the principle floral taxa found in our pollen samples.

The degree of bias toward agricultural habitat varied across sampling dates, and this variation corresponded to taxonomic shifts in pollen collection (Fig. 2). The greatest proportion of urban foraging occurred on 4 September, when pollen samples were dominated by clovers (Trifolium spp.). The sharp decline of urban foraging activity starting 12 September coincided with the taxonomic shift from clovers to goldenrod, the latter evidently being concentrated in the agricultural landscape to the south and west of the apiary (Fig. 3). White clover, due to its prostrate growth habit, can tolerate frequent mowing and is common in urban open areas including residential lawns (Frank and Hathaway 2015) as well as in the field margins and roadsides of the agricultural landscape. In contrast, goldenrod, with its tall growth habit, is restricted to unmowed open areas; in our study region, these include mainly uncultivated fields and conservation strips, consistent with the growth patterns and habitat associations described by Pavek (2011). By mid-September in our study region, the summer-blooming clovers are in decline and goldenrod emerges as the last major pollen and nectar source of the year. In the absence of late blooming urban flora, like the ivy (Hedera helix) common in the UK landscape studied.
by Garbuzov and Ratnieks (2013), strictly urban honey bees without access to other foraging habitat might suffer an early end to their foraging season, as predicted by Burgett et al. (1978) and inferred by Sponsler and Johnson (2015). Urban beekeepers in our study region should, therefore, consider providing supplemental feeding as soon as the major summer flora begin to decline.

The preference of honey bees for agricultural over urban landscapes observed in this study must be interpreted cautiously. Urban landscapes can differ markedly from one another, both within and between cities. In Ohio, for example, the densely developed landscape of Columbus differs strongly from the landscape of nearby Cleveland, which contains extensive ruderal land colonized by adventitious plants. Similarly, agricultural landscapes, even those with the same major crops, can differ significantly in the composition and prevalence of non-crop vegetation, which may provide the bulk of honey bee foraging resources (Requier et al. 2015; Long and Krupke 2016). Nevertheless, the adventitious plants of the agricultural landscape that supported honey bee foraging in our study—particularly clovers and goldenrod—are widely recognized as major pollen and nectar sources throughout much of the U.S. and Canada (Pellet 1920; Goltz 1975; Severson and Parry 1981; Ayers and Harman 1992; Stimac et al. 1997; Long and Krupke 2016), and it is likely that wherever these plants are of prime importance, agricultural landscapes will surpass their urban counterparts in the provision of honey bee foraging resources in the summer and fall. This pattern could potentially be offset by changes in urban land management that would allow flowering plants to grow in areas conventionally maintained as turfgrass, such as residential yards and public greenspaces.

**Data availability statement**

Complete pollen data are available in supplemental material S2. Decoded dance data and GIS layers are available from authors upon request.

**Supplementary data**

Supplementary data, S1–S3, are available at JUECOL online.

**Conflict of interest statement**

None declared.

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