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RESEARCH ARTICLE

Dancing bees evaluate central urban forage resources as superior to agricultural land

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Abstract

1. Recent evidence suggests that flower-rich areas within cities could play an important role in pollinator conservation, but direct comparison of floral resources within agricultural and urban areas has proved challenging to perform over large scales.
2. Here we use the waggle dances of honeybees *Apis mellifera* L. to perform large-scale landscape surveys at heavily urban or agricultural sites for a key pollinator of wild and crop plants. We analysed 2,827 dances that were performed by 20 colonies in SE England.
3. We show that hive median foraging trip distance is consistently lower at urban sites across the entire season. The sucrose content of collected nectar did not significantly differ between urban and agricultural land, ruling out the possibility that longer foraging distances in agricultural sites were driven by distant but nectar-rich resources.
4. Within cities, bees preferentially targeted residential areas on foraging trips, while trips to mass-flowering crops overwhelmingly dominated at agricultural sites. For both land-use types, distances flown increased in the summer, but there was high variation in temporal patterns between individual sites.
5. *Policy implications*. From the self-reported perspective of a generalist pollinator, forage was easier to find in heavily urbanized areas than in the modern agricultural landscapes that we studied. A focus on continuous spatial and temporal provision within agricultural environments is key to redressing this imbalance.

KEYWORDS

Apis mellifera, cities, dance decoding, forage availability, pollinator, urbanization

1 | INTRODUCTION

The most pressing threat facing bee populations world-wide is habitat loss and fragmentation, mediated by agricultural intensification over the last century (Baude et al., 2016; Newbold et al., 2015; Potts et al., 2016). In combination with challenges posed by widespread pesticide use (Wood & Goulson, 2017) and emerging parasites and disease (Fürst et al., 2014), this extensive conversion of flower-rich habitat to land that is often nutritionally barren from the bee's perspective has been strongly implicated as a driver of

FIGURE 1 Location of 10 urban (triangles) and 10 agricultural (squares) observation hives in SE England. The Greater London area is indicated by dark grey shading (inset map). Hives were a minimum of 5,000 m apart to minimize overlap of foraging ranges

pollinator declines (Carvell et al., 2006; Potts et al., 2016; Senapathi et al., 2015). Within this context, growing evidence to suggest that flora-rich patches within cities and towns may support diverse bee populations (Baldock et al., 2019; Hall et al., 2016; Theodorou et al., 2020), and that wild social bee colonies in urban areas may outperform their agricultural counterparts (Goulson et al., 2002; Samuelson et al., 2018; but see Milano et al., 2019) has raised the possibility that cities might offer important refuges in an impoverished agricultural landscape. Although usually surrounded by large expanses of impermeable man-made surface, urban parks, gardens and allotments can offer high floral abundance and diversity across the season (Baldock et al., 2019; Plascencia & Philpott, 2017), alongside rich nectar resources (Tew et al., 2020). However, directly comparing forage availability for bees in urban and agricultural environments through ecological surveying presents a major challenge of both access and scale that can be hard to overcome.

Here, we capitalize upon the unique waggle dances of honeybees to compare the floral resources available to this key pollinator in urban and agricultural environments at the landscape scale. As the most widely managed pollinator species globally, the western honeybee *Apis mellifera* provides crucial pollination services to a broad range of both wild and crop plants (Hung et al., 2018). While *Apis* population trends are likely to be heavily influenced by socio-economic factors (Moritz & Erler, 2016; Potts et al., 2010), there is evidence to suggest that trends for urban honeybees may follow those for wild species, with colonies performing relatively well in urban areas (Lecocq et al., 2015; Samuelson et al., 2020; but see Sponsler & Johnson, 2015). Honeybees are generalists that collect a broad range of resources across a foraging range than can span several kilometres (Beekman & Ratnieks, 2000; Steffan-Dewenter & Kuhn, 2003), and unlike any other pollinator, communicate locations of profitable resources to their nestmates through waggle dances that can also be decoded by human observers. These dances provide filtered real-time information on the resources that colonies have found through a large-scale search effort that has no access limitations (a key hurdle in surveying urban areas; Couvillon, Schürch, & Ratnieks, 2014a, 2014b; Visscher & Seeley, 1982; Waddington et al., 1994).

Waggle dances encode both the distance to the resource (in the duration of the 'waggle' run) and its direction, relative to the sun's azimuth (in the angle of the dance relative to gravity; von Frisch, 1967). Foragers do not dance to report every resource that they find, but only those that pass a quality threshold (von Frisch, 1967), performing more circuits for resources that offer high energetic efficiency (i.e. energy invested in travel – energy gained through food intake; Seeley, 1994). In other words, the closest highly rewarding sites elicit the most dances and thus the most recruits, and support for those sites builds within the hive through a positive feedback loop (von Frisch, 1967). Thus, as long as forage energetic content can be independently validated, the distance to forage indicated by the majority of dances provides a real-time picture of current forage availability, from the bees' own perspective, within the colony's foraging range (Couvillon et al., 2014b).

Previous attempts to compare honeybee dances across urban and rural sites using dance decoding have been limited to two single-site choice-based studies that produced contrasting results (Garbuzov et al., 2015: preference for urban land over rural; Sponsler et al., 2017: preference for agricultural land over urban). Here, we compared median foraging distances from 20 observation hives (2,827 dances) placed at either the urban or the agricultural extremes of an urbanization gradient in SE England (Figure 1), recorded fortnightly (i.e. every 2 weeks) over 24 weeks from April to September 2017. We also analysed 551 dances from a subset of these hives in 2016, to investigate consistency across years. At each session, we also recorded nectar quality (sugar concentration) to validate our assumption that longer foraging trips reflected a dearth of available forage rather than the existence of distant but high-quality sites. By mapping dance distributions onto land-use maps, we also investigated the importance of specific land-use types for floral resource provision within the urban and agricultural sites across the season.

2 | MATERIALS AND METHODS

2.1 | Sites

Following a recruitment campaign targeting beekeeping groups, we selected 20 (*n* = 10 agricultural, 10 urban) existing apiary sites at the extremes of the urbanization gradient in the region, such that our urban locations represented central London rather than suburban areas (Figure 1). All selected sites were located at least 5,000 m apart to minimize overlap of foraging ranges. To confirm differences in land use between urban and agricultural sites, we classified the land at a 2,500-m radius (incorporating the 95th percentile of recorded dances) around each site using QGIS v3.0.2 following methods outlined in Samuelson and Leadbeater (2018). Briefly, we generated land-use maps (Figure 2; Figure S1) by drawing polygons around habitat patches on a satellite imagery (Bing Maps) base layer and classifying these patches into land-use categories (Table S2). To ensure that oilseed rape (OSR), which may not be detected by satellite imagery, were included in our mapping, we additionally performed aerial drone surveys (DJI Phantom 4; DJI, Shenzhen, China; 360° recording from 120 m above the hive) at each agricultural site during May (the OSR bloom period). Urbanized area (Table S2 categories *continuous central*, *dense residential*, *sparse residential* and *built-up area*) comprised 81.95 ± 8.15% (mean ± *SD*) of land area at urban sites and 16.75 ± 10.40% (mean ± *SD*) of land at agricultural sites. Agricultural sites contained 57.72 ± 16.59% (mean ± *SD*) agricultural/arable land (Table S2 categories *arable*, *pasture*, *other agricultural*, *fruit*, *OSR*), of which 5.76 ± 5.37% contained fruit or OSR crops. For a full description of land use at each site, see Table S1.

Dances from each site were videoed once every 2 weeks for 24 weeks between April and September (two sites visited each day between 8:00–12:00 ('a.m.') and 12:00–17:00 ('p.m.') respectively). The same procedure was followed for 2 months (July–August) in 2016 at four of the sites (two urban and two agricultural), to investigate whether foraging distances differed across years within hives. In total, we recorded 2,827 waggle dances (1,428 urban and 1,399 agricultural) in 182 site-fortnight combinations in 2017, and 551 waggle dances in 24 site-week combinations in 2016.

2.2 | Honeybee colonies

An observation hive containing a honeybee colony with three to eight frames of workers, brood and a queen was located at each site. Where there was no existing observation hive, we installed standard three frame hives (two shallow and one deep frame) situated in plastic storage sheds with access to the outside through a clear PVC tube (25 mm diameter). Existing hives (*n* = 10/20; six urban and four agricultural) were left in situ. Colonies were not supplied with extra food unless they were temporarily at risk of starvation during the set-up process (no nectar in storage cells or poor weather), when they received supplementary sugar syrup (50° Brix) in a gravity feeder at the top of the hive. If colonies failed, they were replaced immediately with a new nucleus (*n* = 5 early season failures, all prior to data collection). Colonies were checked regularly by apiary managers to ensure adequate stores were available and inspected thoroughly every 2 weeks. Swarm control (removal of a brood frame and/or queen cells) was carried out between April and July if swarm risk was detected; no colony swarmed during the experiment.

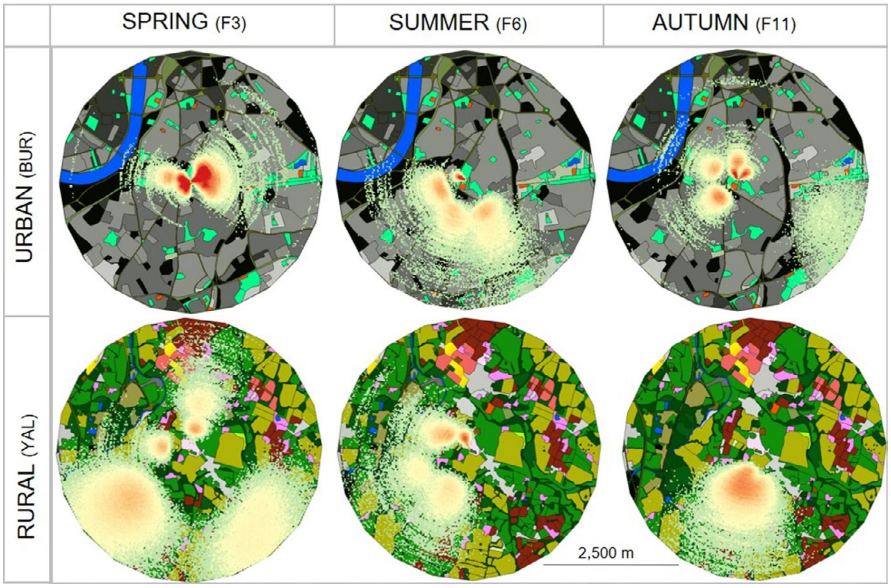


FIGURE 2 Example plots from one urban (BUR) and one agricultural site (YAL). Each circle shows the dances recorded on a single filming period during May, mid-June or early September. Waggle dances are displayed as probability heat maps (Schürch et al., 2013) overlaid on GIS land-use maps (radius 2,500 m) produced for land-use preference analysis. Figure S1 shows the full dataset

2.3 | Data collection

Visit days for video recording of hives alternated between urban and agricultural pairs of sites. The order of visits was kept approximately consistent throughout the experiment (weather permitting) and the period (a.m. or p.m.) of the visit to each hive alternated between fortnightly visits. Sites were visited only on sunny, warm (>12°C) and calm (wind speed <15 km/hr) days to ensure bees were foraging. Temperature data (daily mean) were taken from the London Heathrow weather station (wunderground.com).

On each visit, 2 hr of waggle dance data were recorded by training a camcorder (Canon Legria HF R606) onto the dancefloor area of the hive. Plumb lines to provide a reference for gravity and a radio-controlled clock were attached to the glass in the field of view. At the end of filming, we collected nectar sucrose concentration data by blocking the entrance to the hive and collecting 10 returning foragers that were not carrying pollen (Couvillon et al., 2014b). Following anaesthesia in a cool bag containing ice blocks, we stimulated regurgitation by massaging the bees' abdomens with forceps. Using a microcapillary tube, crop contents were transferred to a 0–80° Brix refractometer (Kern) to measure sucrose concentration.

2.4 | Waggle dance decoding

We decoded up to 40 (mean = 15.5) dances per session (QuickTime 7.1; frame-by-frame playback at 25 fps) following methods outlined by Couvillon et al. (2012). Briefly, we decoded four waggle runs for each dance, excluding the first and last runs, which typically exhibit more variation than middle runs. For each run, we recorded the angle from vertical, calculating the angular displacement from North of the advertised resource by adding the angle to the sun's azimuth at the time of the dance. We measured run duration by recording the first frame in which the bee started vibrating its body and the first frame after the vibration had finished. When a run was interrupted (e.g. by colliding with another bee), that run and the next were skipped. When high dance activity resulted in difficulty keeping track of individual dancers over time, each dance at a single time point was decoded and the video skipped forward 6 min to avoid recording the same dance twice. To convert waggle run durations to foraging trip distances, we used a published universal calibration derived from waggle dance data from two temperate European honeybee populations (https://doi.org/10.7294/tnm4-9123). This calibration is an updated version of von Frisch's (1967) original calibration, and of that used in previous dance decoding studies (Couvillon et al., 2014b), including extra data from hives across more sites, while remaining linear and incorporating variation in distance communication (Schürch et al., 2019).

2.5 | Statistical analysis

To compare colony foraging distance across land-use types in 2017, we analysed log-transformed median waggle run durations (as a proxy for foraging distance) from each video session. Thus, each session represented one single distance data point. To allow for a nonlinear effect of date on the response, we used Generalized Additive Mixed Models (package MGCV; Wood, 2011). We followed an information theoretic model selection approach, first creating a base model that included a smooth for Day of the Year, plus recording period (a.m./p.m.), colony strength (bee-covered surface) and residual temperature (residuals of a simple GAM predicting temperature based on Day of the Year, to avoid concurvity between temperature and date; Graham, 2003) as fixed linear predictors. To incorporate the random effect of Site, we included smooths for s(Site) and s(Site, Day_of_Year), specifying the smooth type as 'random effect' (i.e. a penalized parametric term). Our candidate model set for comparison included this model (the null hypothesis) and three other candidate models containing the same variables but additionally:

1. Separate intercepts for the two land-use types, representing the hypothesis that waggle run duration differs between urban and agricultural land.
2. Separate intercepts and separate date smoothers for urban and agricultural site types, representing the hypothesis that temporal patterns in duration also differ across land-use categories.
3. Separate date smoothers (but not intercepts) for urban and agricultural site types, representing the hypothesis that temporal patterns differ between land-use categories, but the overall means do not differ.

Model comparisons were based on AICc. Where model selection identified competing top models (ΔAICc from top model <2), we selected the simpler model. Nectar quality (sugar content, °Brix) was analysed using the same approach. We excluded zero values (2.6% of samples; 2.1% agricultural, 3.3% urban) as these indicate bees that were collecting water (Couvillon et al., 2014b).

Final models were examined for spatial autocorrelation by using a Moran's I test on the residuals and graphically assessing the spatial pattern of residuals. The adequacy of the number of basis functions (k) for each smooth function was assessed by comparing k to the effective degrees of freedom (EDF); where k fell close to the EFD (as indicated by k-index p-values <0.05, obtained via gam.check in R-package MGCV), we increased k until no detectable pattern existed in the residuals.

To examine whether distance flown might vary across years for individual hives, we also compared waggle run duration (log-transformed medians per hive as above) between 2016 and 2017, for the four hives that featured in both years (linear model; $n = 37$ sessions; 24 sessions from 2016 and 13 from 2017). Only July and August data were included for the 2017 dataset, to ensure a match in sampling period for the 2 years. Given the restricted size of the dataset, we included a reduced set of predictors that included only site, year and their interaction as fixed factors.

2.6 | Land-use preference analysis

The differences that we found in foraging distance between urban and agricultural hives led us to investigate which of the land-use types within these differing landscapes received most attention by foraging bees during different seasons (spring: April–May, summer: June–July, autumn: August–September). For each site, we produced a land-use raster of radius 2,500 m (incorporating the 95th percentile of recorded dances) and resolution 25 m (Figure 2). The raster separated land-use patches into broad categories selected for ecological relevance to pollinator use of the landscape (Samuelson & Leadbeater, 2018), combined from land-use classes in our initial GIS classification. In agricultural landscapes the categories were built-up, non-agricultural, woodland, arable, pasture, fruit, OSR and other agricultural; in urban landscapes the categories were continuous urban, dense residential, sparse residential, parks, amenity grassland, railway, woodland and watercourses (Table S2 describes constituent land-use types within each category).

Variation between repeated waggle runs of the same dance means that a single dance does not pinpoint a single unique location. Thus, to predict where bees had foraged, for each single site-season combination, we simulated a single foraging location (eastings and northings) for each recorded dance (mean n = 47.86 ± *SE* 3.22), following methods outlined in Schürch et al. (2013). Each land-use patch (i.e. each raster square from the land-use raster) was recorded as visited or not visited by one or more of the simulated foraging visits, along with its area and distance of nearest edge to the hive. This was repeated for each site in a landscape-season combination, for example spring data for all sites in urban landscapes. A binomial GLMM (logit link function) was constructed with 'visited' as the response and land-use and distance as fixed effects, alongside a random effect of site ID. The adjusted odds ratios (AORs) for visitation of each land-use type relative to the baseline type (selected as the most urban land-use type: 'continuous urban' in urban landscapes, 'built-up' in agricultural landscape), corrected for distance to the hive, were extracted from the model. This procedure was simulated 1,000 times, and repeated for each of the six landscape-season combinations, using packages ASCII (Hajage, 2020), RASTER (Hijmans, 2021), SP (Bivand et al., 2013), RGDAL (Bivand et al., 2018) and RGEOS (Bivand & Rundel, 2020).

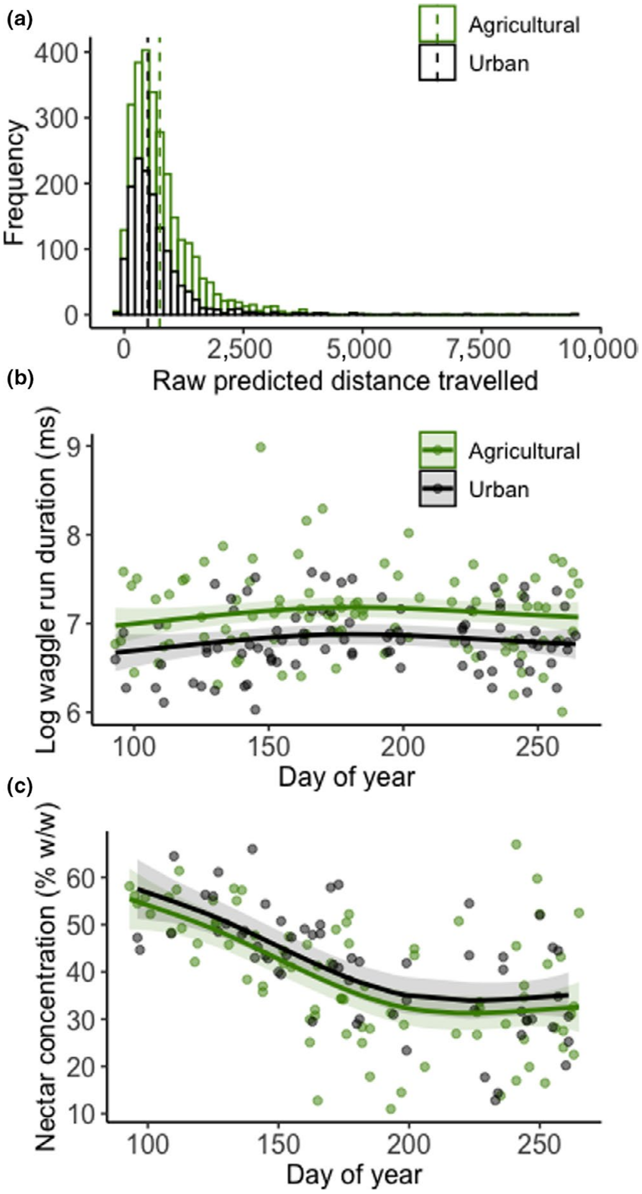


FIGURE 3 Foraging behaviour of urban and agricultural hives. (a) Distribution of distances travelled (predicted from waggle run durations) for urban and agricultural colonies. Dotted lines represent medians for each land-use type; (b) Log-transformed waggle run durations (ms; medians per observation session); (c) Concentration of nectar (%w/w; medians per observation session) from sampled returning workers. Solid lines are provided for visualization and indicate smoothed predictions obtained from GAMs that included only separate intercepts for each land-use type plus a nonlinear relationship between Day of the year and median waggle run duration or nectar concentration (i.e. Duration/Concentration ~s(Day + Land Use), with shaded areas indicating 95% confidence intervals (*ggplot2*; Wickham, 2016)

3 | RESULTS

3.1 | Distance to forage and nectar quality

In both land-use types, most flights were relatively short distance relative to the maximum foraging range (Figure 3a; Figure S2; Urban: median translated foraging distance = 492 m, max = 9,375 m; Agricultural: median = 743 m, max = 8,158 m). Across the whole season, we found a strong overall effect of land use on median hive waggle run duration, implying that bees flew further to find forage in agricultural landscapes (Figure 3b; urban land-use parameter estimate relative to agricultural baseline [*SE*]: −0.34 [0.11]; Table S3). For both land-use types, distance flown increased slightly in the summer months, but we found no strong evidence that this relationship varied across land-use types (including separate smoothers for agricultural and urban land improved the fit of the model by <2 AICc units, Table S3). Indeed, the inspection of the data for individual sites suggested high variation in temporal patterns between sites across both land-use types (Figure 4). There was no effect of colony strength, residual temperature or filming period on waggle run duration (ΔAIC of model containing none of these predictors against final model = 0.52), and repeating the analysis with these variables removed from all candidate models made no qualitative difference to the results. When we compared the distances covered in 2017 with those travelled in the same period in 2016, for the four hives that had been sampled in both years, we found no significant effect of year on distance travelled (model-averaged parameter estimate for 2017 vs. 2016 [*SE*]: 0.06 [0.11]; Table S4).

The analysis of the nectar collected by returning foragers showed that longer flights in agricultural landscapes were not compensated for by collection of high-quality resources (Figure 3c). Including separate intercepts for the two land-use types improved the base model, but not significantly so (ΔAICc = 1.91; Table S3), and further inclusion of separate smoothers led to a drop in AICc (ΔAICc = 15.15; Table S3). Thus, while nectar concentration followed a nonlinear pattern across the course of the year (Figure 3c), peaking in the spring and decreasing towards the summer months, this pattern was similar across the two land-use types.

3.2 | Land-use preference

The analysis of preference for small-scale land-use types within the wider urban and agricultural landscapes highlighted reliance on residential gardens in urban areas and mass-flowering crops in agricultural areas (Figure 5). Specifically, bees in urban areas showed a preference for sparse residential land (discontinuous development typified by large total garden area, Table S2) across the whole season (spring odds ratio (OR) [95% CIs]: 5.4 [3.0 to 10.0]; summer: 4.6 [2.9 to 7.2]; autumn: 4.2 [2.6 to 6.8]) and a relatively smaller yet significant preference for dense residential land (discontinuous development with a high ratio of impervious surface to gardens; spring OR: 2.4 [1.3 to 4.3]; summer: 3.4 [2.1 to 5.8]; autumn: 3.3 [1.9 to 5.5]). In agricultural areas in spring, bees showed a strong preference for OSR (OR: 24.8 [13.0 to 46.0]), and weaker preferences for arable land and fruit crops in all time periods; Arable: spring OR 6.4 [3.9–11.1], summer 9.3 [6.4–13.7], autumn 7.6 [4.5–12.2]; and Fruit OR 5.7 [2.4–11.1], summer 4.4 [2.0–8.7], autumn 4.9 [1.5–11.0]. Pasture was also slightly but significantly preferred: spring OR 3.0 [2.0–4.7], summer 3.4 [2.4–4.9], autumn 2.0 [1.7–4.5].

4 | DISCUSSION

Despite being surrounded by land dominated by man-made surfaces, the urban honeybees in our study had to travel significantly less far to find food throughout the season than those in agricultural areas, suggesting that urban areas provided consistently more available forage. The overall increased foraging distances covered by bees in agricultural land were not recompensed by increased nectar sugar content, which did not differ significantly between the two land-use types. In other words, agricultural bees did not fly further to exploit distant but richer nectar resources than those available to their urban counterparts, but rather, typically came back with similar quality forage, at least in terms of nectar concentration. Our findings demonstrate the potential value of urban forage resources within intensified agricultural landscapes for *Apis mellifera*, a key pollinator of both crops and wild flowers.

Our data revealed that bees travelled further to find forage in the drier summer months, as would be expected in a temperate European landscape, and in accordance with seasonal patterns in foraging distance reported by other studies (Couvillon et al., 2014b;

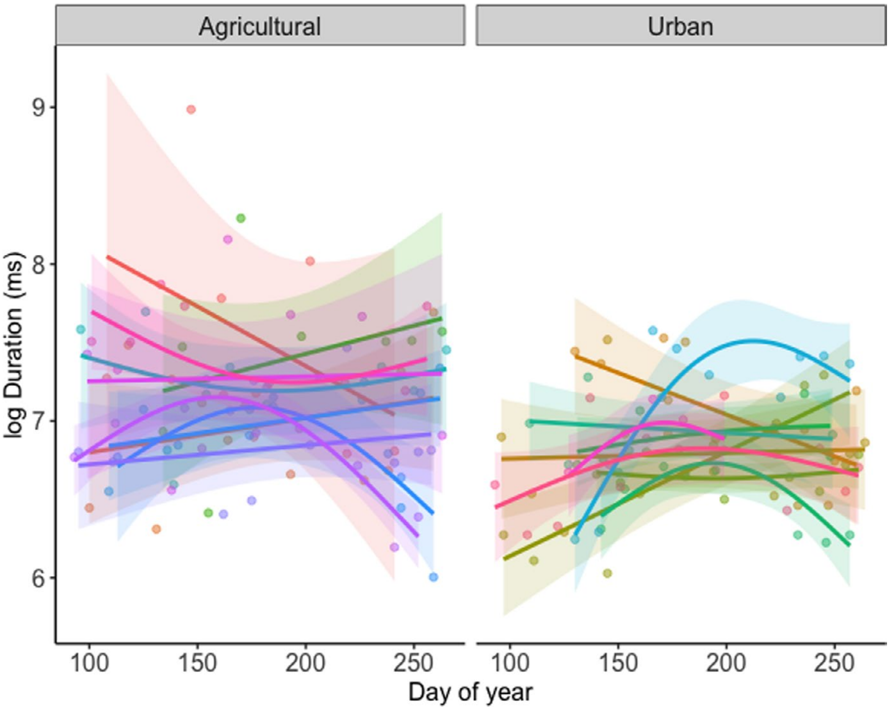
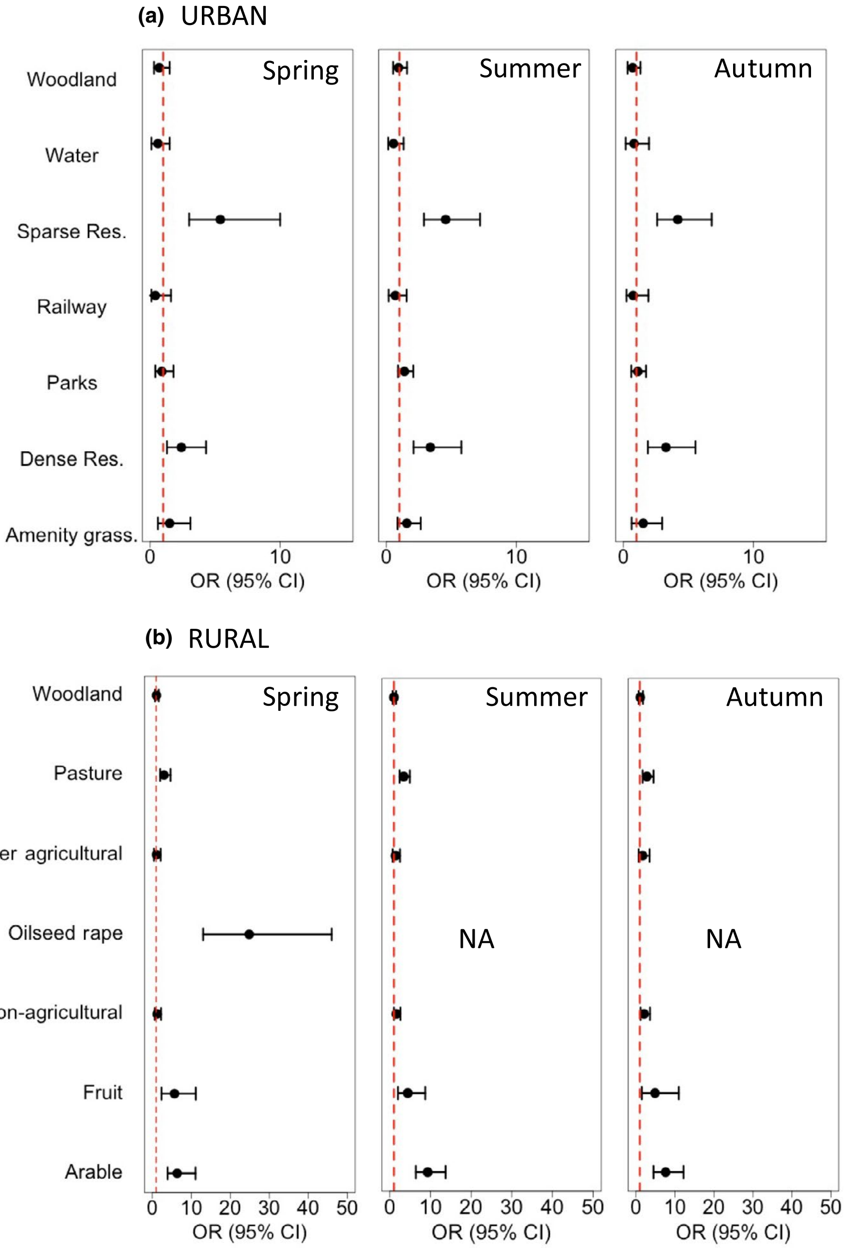


FIGURE 4 Temporal variation in log waggle run duration (ms; median per observation session) across sites (*n* = 10 urban, 10 agricultural). Lines are smoothed conditional means for each site from a GAM allowing for separate nonlinear effects of Day of Year on log waggle run duration for each site (function geom_smooth in *ggplot2*; Wickham, 2016)

FIGURE 5 Adjusted odds ratios (±95% CIs) for visitation to land-use types within urban (a) and agricultural (b) landscapes. Error bars that do not cross an odds ratio of 1 (red line) indicate significant differences from the baseline land-use type ('Continuous Urban' in Urban and 'Built-Up' in Agricultural). Data from fortnights 1–4 (spring), 5–8 (summer) and 9–12 (autumn) are pooled



Danner et al., 2016; Leong & Roderick, 2015). Nonetheless, we observed considerable variation in temporal patterns across sites, highlighting that both agricultural and urban environments are patchy and conditions will vary according to resource proximity. For urban land, this may represent variation the proximity of apiaries to allotments and gardens, which represent hotspots of diversity for bees (Baldock et al., 2019; Theodorou et al., 2020), provide rich nectar resources (Tew et al., 2020), and were identified by our land-use preference analysis as targets for visitation. Management strategies for urban land could therefore focus on further improvement in this provision through educational campaigns promoting native flowers in horticulture, given that many gardens are dominated by ornamentals that fail to attract insects (Garbuzov & Ratnieks, 2014). For agricultural areas, our land-use preference analysis highlighted reliance on mass-flowering crops in agricultural landscapes (Danner et al., 2016; Requier et al., 2015); OSR clearly attracted a large proportion of visits during the spring, but fruit crops were also consistently visited throughout the year. However, pasture also contributed (albeit to a much lower extent than OSR), potentially because such land may also have contained field borders, flowering trees and weeds. Such areas are a potential target for measures aiming to improve pollinator forage on agricultural land.

The longer distances flown by bees in agricultural areas cannot be explained by the presence of distant but high-quality sites, because bees in agricultural areas flew further only to return with similar quality nectar. However, we cannot rule out the existence of high-quality distant pollen resources. Pollen quality is complex to quantify, and varies discretely between plant species, depending on protein, amino acid, lipid and sugar content. Pollen diversity (rather than simply the nutritional value of single species in isolation) also contributes to bee health (Di Pasquale et al., 2013). However, we have previously found (using a larger sample of apiaries that included some of those in the current study) that the diversity of stored pollen is greater in urban than agricultural settings (Samuelson et al., 2020). The same study found urban honeybee colonies to be stronger than their agricultural counterparts, with less prevalence of *Nosema* infection, but results for other pathogens are mixed, and for other bee species evidence relating urbanization to pathogen loads is unclear (Goulson et al., 2012; Samuelson et al., 2018; Theodorou et al., 2016). Thus, it is not year clear whether higher forage availability in urban land directly contributes to colony success in such areas. Insecticide exposure is also likely to differ between urban and agricultural land-use type, but residue levels and associated risks of horticultural versus agricultural environments remain to be investigated from this perspective, and constitute a pressing area for future study. Likewise, urban and agricultural environments are likely to be associated with different levels of other pollutants, the effects of which remain unknown.

Dance decoding is a unique survey method that relies upon a bee's own perception of the direction and distance that she has flown, the latter of which is measured through optic flow (Srinivasan et al., 2000). In complex landscapes, the same distance will elicit greater optic flow, and thus may be perceived as further, leading to longer central waggle runs (Tautz et al., 2004). It is thus possible that we overestimated the relative distance flown for complex landscapes, and underestimated it for simpler ones, given that we used a universal linear converter (Schürch et al., 2019). Since we expect urban sites to be more complex than agricultural ones, our results may thus be a conservative estimate of the differences between urban and agricultural land. Overall, the impact of urban landscapes on bee flight trajectories is an area that invites further study.

Although *A. mellifera* is a critically important pollinator for both agricultural crops (Calderone, 2012) and plants in natural habitats (Hung et al., 2018) world-wide, declining *Apis* population trends can be to some extent mitigated through beekeeping practices (but see, Potts et al., 2010). This is not the case for wild bees, which are key to ecosystem health (Garibaldi et al., 2013). Our findings are difficult to generalize to solitary or specialist species, for which the presence of particular flower species as larval food sources, or nest site availability, may well be critical (Biesmeijer et al., 2006; Steffan-Dewenter & Schiele, 2008). While such species typically have much short foraging ranges than honeybees and so may be particularly challenged in patchy agricultural landscapes, their forage availability is also likely to vary at a fine scale across urban landscapes, making it hard to draw conclusions across ‘urban areas’ as a whole. On the other hand, such species may be particularly vulnerable to dearth periods because unlike social bees, they cannot store resources gathered at times when resources were more plentiful. However, for generalist social bees, including several *Bombus* species, our evidence suggests that cities may offer plentiful floral resources within barren agricultural land (Baldock et al., 2019; Samuelson et al., 2018; Theodorou et al., 2020).

The availability of urban green space varies both between and within cities (Kabisch et al., 2016), and our results from urban sites that were specifically chosen to represent the extreme, central end of an urbanization spectrum (Figure 1) most likely underestimate the floral resources available in more suburban areas, which may be a particularly valuable resource. On a wider scale, given that northern European cities such as London typically contain relatively high green space availability (Kabisch et al., 2016), our findings support that urban planning that prioritizes residential green space could increase the value of urban areas for social bees in cites that are less garden-rich. Nonetheless, urban land remains a small percentage of total land cover, and islands of potentially abundant forage are unlikely to be sufficient to support bee populations across a landscape dominated by intensive agriculture. As such, in the long term, conservation efforts should be primarily directed towards increasing non-crop floral provision in agricultural areas, such as wildflower strips (Williams et al., 2015), to increase consistency of forage availability across the season and the landscape, minimizing reliance on small numbers of ephemeral flowering crops. Our study harnesses the unique habitat surveying capability of the honeybee waggle dance to demonstrate that cities can provide islands of forage within relatively barren agricultural land, but since crop plants are located outside cities, redressing this balance through improved floral provision on agricultural land will be critical to healthy ecosystem service provision.

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CONFLICT OF INTEREST

The authors have declared no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.E.S. and E.L. conceived the initial idea and designed the experiment; A.E.S. performed the experiment; A.E.S., E.L. and R.S. performed the statistical analyses; A.E.S. and E.L. wrote the manuscript and E.L., R.S. and A.E.S. provided the final edit.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.c2fqz618f (Samuelson et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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