

# Eating locally: dance decoding demonstrates that urban honey bees in Brighton, UK, forage mainly in the surrounding urban area

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**Abstract** Urbanization is increasing worldwide. Urban habitats often support considerable biodiversity and so are of conservation value, even though they are highly modified ecosystems. Urban parks and gardens are rich in flowers that provide food for pollinators, including bees. Here, we use waggle dance decoding to investigate foraging by 3 honey bee hives located in the city of Brighton, UK, over almost an entire foraging season, April to October. Waggle dances were recorded using video cameras and decoded during framewise playback on a computer by measuring the angle and duration of the waggle phase. Foraging was mostly local (mean monthly distances 0.5–1.2 km) and mostly within the surrounding urban area (monthly means 78–92 %) versus the countryside (closest distance 2.2 km) even though this was well within the honey bee maximum foraging range (c. 12 km). These distances were lower than those from a previous study for hives located in a rural area 4.5 km away. Honey bees are very sensitive to foraging economics and foragers make waggle dances only after visiting high-quality feeding locations. Low distances advertised by dances, therefore, indicate sufficient forage nearby and show that urban areas can support honey bees year round. As a corollary, however, urban bees may provide little pollination service to agriculture especially in spring, which had the lowest foraging distances and is when the most economically important animal-pollinated UK crops, apple and oilseed rape, are in bloom.

**Keywords** Floral resources · Pollination · Urban ecosystems · Waggle dance

## Introduction

Urban and suburban areas cover 0.4 % of the ice-free land area worldwide (Ellis et al. 2010), but more in the UK (6.8–9.5 %, depending on definition; UK National Ecosystem Assessment

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2011). More than half (51 %) of the world's population now lives in urban, rather than rural areas, and this is projected to increase to 68 % by 2050 (United Nations 2012). Urban habitats are highly modified and are generally inferior to natural or semi-natural ones for most types of wildlife (McKinney 2008). Nevertheless, urban areas can support considerable biodiversity (Angold et al. 2006; Davies et al. 2009; Bates et al. 2011) and are of current interest in conservation (Dearborn and Kark 2010; Sanderson and Huron 2011) and the emerging field of urban ecology (Gaston 2010; Niemelä 2011).

Urban gardens, parks and other green spaces contain flowers which can provide food for pollinators, such as bees, butterflies and hover flies (Kadlec et al. 2008; Goddard et al. 2010; Matteson and Langellotto 2010; Hennig and Ghazoul 2012). In some urban areas beekeepers can make good honey crops (Burgett et al. 1978). In the UK, urban beekeeping is increasingly popular, with the number of managed colonies in London tripling to over 3,500 during the past 5 years (Alton and Ratnieks 2013).

Honey bee foragers use the waggle dance to communicate the locations of food sources to their nestmates (von Frisch 1967). Each dance provides a vector (direction and distance) from the nest to the dancer's foraging location (Riley et al. 2005). Since bees only dance to advertise the most profitable food sources, the dances present filtered information about the most profitable foraging locations known to a colony at that time (Seeley 1994, 2012). By decoding many dances, it is possible to build up a picture of where a colony or a group of colonies is foraging and how this changes with time. Thus, waggle dance decoding is a powerful and unique methodology for studying honey bee foraging.

Most previous studies using dance decoding to investigate honey bee foraging focused on agricultural or natural landscapes and typically restricted their data collection to just a few months of a longer foraging season (e.g. Visscher and Seeley 1982; Steffan-Dewenter and Kuhn 2003). Here, we decoded dances from 3 urban hives over most of an entire foraging season, April to October, to explore urban foraging and for comparison with similarly collected data from hives located 4.5 km away in a rural location (Couvillon et al. 2014).

## Materials and methods

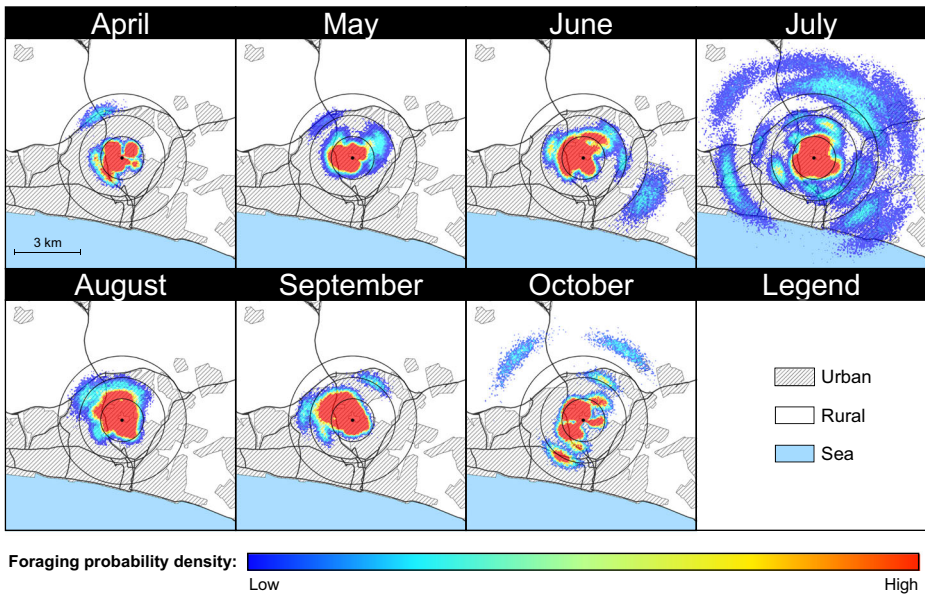
### Study location and honey bee colonies

We studied three honey bee colonies housed in glass-walled observation hives located at an environmental studies building of a local school with a special interest in conservation (Dorothy Stringer School, latitude: 50.849370, longitude: -0.14167996) in Brighton, UK, a city that is part of a conurbation of 474,000 residents (Office for National Statistics 2011). The school is in the north-central part of the urban area, c. 2.2 km from countryside (see Fig. 1).

Each hive had three medium and one deep Langstroth frames, an egg-laying queen, brood of all ages, and c. 2,000–5,000 workers. Worker bees and brood were removed as necessary to prevent swarming, which is triggered by overcrowding. To prevent possible starvation, colonies were fed 500 ml of 2 M sugar solution most weeks after videoing for data collection (see below), so that the syrup had been consumed several days before data collection resumed.

### Waggle dance analysis

Colonies were monitored from 20 April to 16 October in 2011, which encompasses most of the foraging season (March/April–October/November) in the UK. The dance area of each hive



**Fig. 1** Seasonal variation in probability density distributions of urban honey bee foraging from April to October 2011, as determined by waggle dance decoding. Circles, radius 1, 2, 3 km, are centred on the location of the 3 study hives at the Dorothy Stringer School, Brighton, UK. Colour spectra show the range of relative foraging probabilities, as determined by simulated waggle dance locations, binned into  $25 \times 25$  m quadrats, from blue (1) to red (632–3272, depending on month)

was video-recorded, 25 frames per second, for 1 h at approximately weekly intervals using video cameras (Canon Legria HV40) between 10:00 and 16:00 BST during favourable foraging weather ( $>15$  °C, no strong wind, no rain). Individual dances were analysed by framewise playback on an iMac computer using MPEG Streamclip v.1.9.2 freeware. Up to 20 waggle dances per hour were analysed following the methods of Couvillon et al. (2012), where four middle, consecutive waggle runs per dance are decoded to obtain mean duration, which encodes distance, and mean angle, which encodes direction.

Distance was estimated using a Bayesian linear calibration model built for our honey bee population in the nearby landscape (Schürch et al. 2013), which takes into account the imprecision inherent in the honey bee dance (Couvillon 2012). Probability distributions for both vector component estimates (distance and direction) were obtained by simulating each decoded dance 1,000 times, which enabled us to map the foraging locations shown by the dances in a manner that includes the uncertainty in the dance vector (Schürch et al. 2013). This methodology also allowed us to determine confidence intervals for our estimates of the proportion of foraging in urban versus rural areas. The definition of urban areas followed the Ordnance Survey maps for GIS (vector ‘Meridian 2’) provided by Digimap service (EDINA, <http://digimap.edina.ac.uk>).

All statistical analyses were performed in R. v.3.0.2 (R Core Team 2013). The effects of month as a fixed factor on the responses of the average foraging distance and the proportion of urban foraging were analysed using General Linear Mixed Models (GLMM, function *lme*, package *nlme* (Pinheiro et al. 2013), as described by Zuur et al. (2009)), with ‘colony’ included as a random factor to account for any non-independence of data within colonies. The proportions of urban foraging associated with each waggle dance were estimated by averaging over 1,000 simulations (see above), thus yielding

one independent proportion estimate per dance. These estimates were arcsine square root transformed prior to analyses. Months were compared pairwise using post-hoc Tukey's HSD test (function *glht*, package *multcomp*, Hothorn et al. 2008). All values reported are means  $\pm$  95 % confidence interval.

## Results

### Foraging distance

Mean estimated foraging distances ranged from 461 m in May to 1,229 m in July (Table 1), differing significantly among months ( $L=124.09$ ,  $df=6$ ,  $P<0.001$ ). The addition of colony as a random factor did not significantly improve the fit of the model ( $L=2.96$ ,  $df=1$ ,  $P=0.085$ ), indicating that there were no strong differences among colonies (Fig. 2). The results of Tukey's post-hoc pairwise comparison test are shown in Fig. 3a. Average distance was under 1 km throughout the season, with the exception of July, when it peaked at 1,229 m (Table 1, Fig. 3a). There was also a slight increase in estimated foraging distance in October (Table 1, Fig. 3a). This pattern can also be seen in the distribution maps (Fig. 1).

### Proportion of foraging in urban areas

As the colonies were located 2.2 km from the nearest rural border, foraging at mean distances less than 1.2 km meant that most was in the urban area (78–92 %; Table 1, Figs. 1, 3b). Differences among months were significant ( $L=32.38$ ,  $df=6$ ,  $P<0.001$ ), but not among colonies ( $L<0.001$ ,  $df=1$ ,  $P=0.999$ ). Tukey's post-hoc pairwise comparison test showed no clear linear pattern across time. As expected, the results followed mean foraging distance, with lower proportions of urban foraging in months when the foraging distances were greatest (e.g. July, October) and vice versa in months when mean foraging distances were short. The negative correlation, however, was not significant, although borderline (Pearson's  $r=-0.71$ ,  $P=0.074$ ,  $n=7$ ).

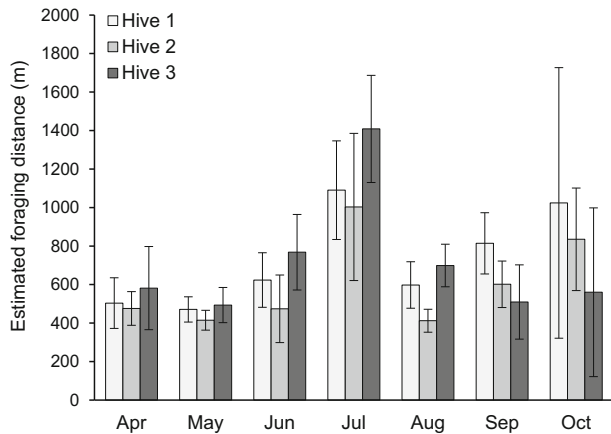
**Table 1** Seasonal variation in honey bee foraging patterns in an urban environment

Month	Estimated foraging distance (m)		Proportion of foraging in urban areas			Number of waggle dances
	Mean	95 % CI	% <sup>a</sup>	95 % CI <sup>b</sup> lower	95 % CI <sup>b</sup> upper	
April	518	86	91.8 %	82.6 %	96.0 %	61
May	461	41	87.0 %	82.2 %	90.7 %	234
June	670	110	87.0 %	79.8 %	91.9 %	116
July	1,229	175	79.9 %	73.9 %	84.7 %	209
August	589	64	83.1 %	76.7 %	87.9 %	166
September	685	96	87.1 %	79.0 %	92.2 %	95
October	846	235	77.8 %	64.7 %	86.9 %	50

<sup>a</sup> Percentage among simulated locations

<sup>b</sup> Agresti-Coull 95 % confidence intervals, where  $p$  (number of simulated locations in urban areas) and  $n$  (total number of simulated locations) are scaled back to the number of waggle dances decoded

**Fig. 2** Seasonal variation in estimated foraging distance in each of three honey bee hives, as determined by waggle dance decoding (bar heights are means $\pm$ 95 % CI)

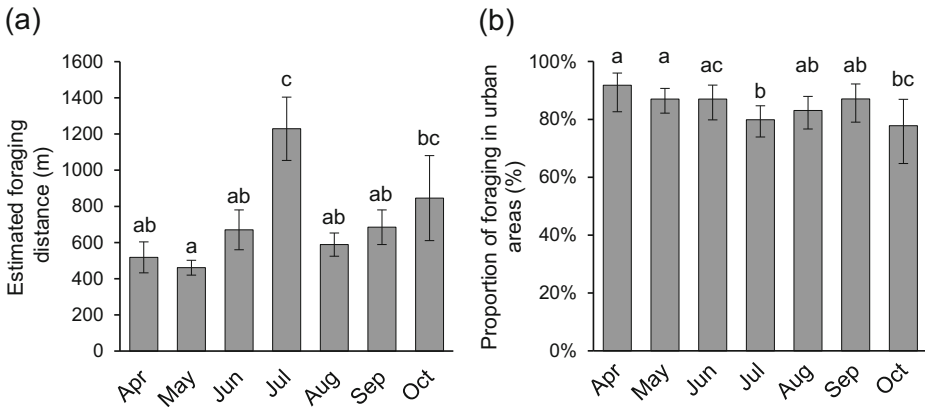


## Discussion

Our results clearly show that most foraging from the urban colonies was at relatively short distances (monthly means 0.5–1.2 km) and thus within the surrounding urban area year round (78–92 %), even though the countryside was well within honey bee foraging range (Ratnieks 2007). In contrast, colonies at the neighbouring rural location (4.5 km distant on the University of Sussex campus) had higher foraging distances except in April and May, when distances were low and comparable with our data, indicating abundant high-quality forage within short distances of both apiaries (Couvillon et al. 2014). In the urban colonies, the mean foraging distance had no clear pattern across time and showed a single-month peak in July (1.2 km), while in the rural hives distances increased from spring (March–May, 0.5–1.0 km) to late summer (July–August, 1.5–2.5 km) and then declined in autumn (September–October, 0.7–1.5 km) (Couvillon et al. 2014).

Beekman and Ratnieks (2000) showed that bees located in the city of Sheffield, UK, will travel many kilometres (mean 5.5 km) to forage in the countryside in August. At this time and in this area the countryside provides exceptional foraging opportunities. It is the peak bloom time of heather (*Calluna vulgaris*), which covers many square kilometres of the moors in the Peak District to the west of Sheffield. Heather is a major UK honey crop (Crane 1976), with beekeepers deliberately moving hives to heather moors (Hooper 1991). However, in May of the following year, the mean distance dropped to 1 km, very similar to the results of this study and that of Couvillon et al. (2014). Although the summer foraging distance difference between Brighton and Sheffield may be because the urban area in Sheffield is poorer in forage than Brighton; this is unlikely as the areas where the hives were kept were very similar residential areas with many houses with gardens and parks. The more likely explanation is that the countryside to the west of Sheffield is exceptionally rich in forage due to the heather moors. In contrast, the countryside around Brighton not only lacks heather moors or similar large flower patches, but is also dominated by intensive agriculture typical for present-day Britain (Robinson and Sutherland 2002).

To our knowledge, the only other dance-decoding study looking at honey bee foraging from hives in an urban location is that of Waddington et al. (1994). Their data were collected in suburban areas of Miami (FL) and Riverside (CA), USA, in spring. As these areas have considerably different environment and climate to the UK, a straightforward comparison is confounded. However, with this reservation, the short foraging



**Fig. 3** Seasonal variation in estimated **a** honey bee foraging distance, as determined by waggle dance decoding (bar heights are means $\pm$ 95 % CI) and **b** proportion of foraging in the urban areas (bar heights are proportions $\pm$  95 % Agresti-Coull CI, which are not symmetrical around the proportion; Brown et al. 2001)

distances reported (0.7–1.4 km) are in close agreement with the spring data in and around Brighton (in accordance with our results and those of Couvillon et al. 2014) and Sheffield (Beekman and Ratnieks 2000).

What does foraging by urban honey bees tell us about urban areas? The low foraging distances shown by our urban bees indicate that colonies were able to find high-quality forage nearby (Seeley 1994; Seeley 1995), and for the most part did not need to visit the countryside, even though it was within foraging range. They also indicate that urban bees may not make a significant contribution to agricultural pollination, especially in spring when two of the most important UK crops benefitting from bee pollination, oilseed rape and apples, are in bloom (Mwebaze et al. 2010). However, our study was conducted in only one urban location and so should be replicated in other locations before generalizations are made.

Urban areas in the UK contain many green spaces, including domestic gardens (Loram et al. 2007), which, collectively, are a large and important resource for wildlife (Davies et al. 2009; Goddard et al. 2010; Cameron et al. 2012). Indeed, many gardeners practice wildlife-friendly gardening, which, among other things, includes cultivating garden plants attractive to flower-visiting insects (Table A1.57 in Mew et al. 2003). The urban area surrounding our study location was largely residential, but even residential areas in the UK are substantially green, as most homes (87 %, Davies et al. 2009) have a garden. The surrounding area also included several public parks, sports grounds including a golf course, and allotments, where honey bees could contribute to crop pollination. In addition to garden plants, many urban trees, such as limes (*Tilia* spp.), willows (*Salix* spp.) and maples (*Acer* spp.), can also serve as important nectar and pollen sources (Batra 1985; Pawlikowski 2010; Çelemlı 2012). In autumn (September – October), the most important source of nectar and pollen is flowering ivy (*Hedera helix* and *H. hibernica*), which is widespread in Britain and abundant in the study area (Metcalf 2005; Garbuzov and Ratnieks 2014).

Are urban areas better than rural areas? Honey bees are very sensitive to foraging economics (Seeley 1995; Seeley et al. 2000; Seeley 2012). As a result, flower patches in the closer urban area would be selected over equal forage-quality patches in more distant rural areas. Therefore, our data showing that most foraging is in the urban area does not mean that this area is better overall, but it does show that it is relatively better after distance is taken into account, as distance is one of the most significant costs associated with a honey bee decision-making in foraging.

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