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Report

Dancing Bees Communicate a Foraging Preference for Rural Lands in High-Level Agri-Environment Schemes

Margaret J. Couvillon,[1,*] Roger Schürch,[1,2] and Francis L.W. Ratnieks[1]
[1]Laboratory of Apiculture and Social Insects, School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK
[2]Evolution, Behaviour, and Environment, School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK

Summary

Since 1994, more than €41 billion has been spent in the European Union on agri-environment schemes (AESs), which aim to mitigate the effects of anthropomorphic landscape changes via financial incentives for land managers to encourage environmentally friendly practices [1–6]. Surprisingly, given the substantial price tag and mandatory EU member participation [2], there is either a lack of [1] or mixed [1, 2, 7] evidence-based support for the schemes. One novel source of data to evaluate AESs may be provided by an organism that itself may benefit from them. Honeybees (*Apis mellifera*), important pollinators for crops and wildflowers [8, 9], are declining in parts of the world from many factors, including loss of available forage from agricultural intensification [10–13]. We analyzed landscape-level honeybee foraging ecology patterns over two years by decoding 5,484 waggle dances from bees located in the center of a mixed, urban-rural 94 km^2 area, including lands under government-funded AESs. The waggle dance, a unique behavior performed by successful foragers, communicates to nestmates the most profitable foraging locations [14–16]. After correcting for distance, dances demonstrate that honeybees possess a significant preference for rural land managed under UK Higher Level AESs and a significant preference against rural land under UK Organic Entry Level AESs. Additionally, the two most visited areas contained a National and Local Nature Reserve, respectively. Our study demonstrates that honeybees, with their great foraging range and sensitive response to forage quality, can be used as bioindicators to monitor large areas and provide information relevant to better environmental management.

Results and Discussion

Insect Pollinator Declines Are Linked to Agricultural Intensification of the Rural Landscape

In the United Kingdom, post-World War II intensification of farmland, such as the elimination of most hay meadows that supported abundant wildflowers, has resulted in a reduction of available forage to provide nectar and pollen for insect pollinators [17, 18]. This has been linked to declines in honeybees, bumblebees, other bees, hoverflies, and butterflies [10–12, 19, 20], which in turn has spurred an immense amount of scientific interest, industry involvement, and government initiatives to increase forage and to conserve habitats [10, 11, 19, 21]. This ever-increasing interest in mitigating the effects of anthropomorphic landscape changes affecting wildlife often takes one of two approaches. One approach is to set aside important wildlife and natural feature areas as National Parks or National Nature Reserves. Another approach is to make existing agricultural land more wildlife friendly by encouraging farmers and land managers to adopt environmentally friendly practices via financial incentives, such as the European Union agri-environment schemes (AESs) [2, 5]. AESs may therefore play an important role in sustaining pollinator populations. However, in the past, it has been difficult to demonstrate even the general value of AESs to improving the rural landscape for nature [1, 2, 7, 22–24].

Honeybees Indicate Foraging Profit over a Large Area, but Distance Must Be Considered

Honeybees (*Apis mellifera*) possess great potential for monitoring the landscape for floral resources. One reason is their long-distance foraging range of ~10 km from the hive [14, 25]. Bees from a single location can therefore survey a large area (almost 100 km^2 in this study; Figure 1). Even more important is the waggle dance, a behavior unique to *Apis* bees. A honeybee forager can communicate to nestmates a distance and direction vector from the hive to the location where she is foraging via the "waggle run" component of the dance [14, 16]. Crucially, at any given time, only foragers working the most profitable patches make waggle dances [14–16]. Dance decoding therefore provides integrated, filtered information about the best forage available, as known to the many thousands of foragers in each colony. This real-time information can then be observed and decoded by "eavesdropping" researchers to evaluate and map the best and, conversely, worst foraging areas across a landscape [14, 25, 26].

We decoded and analyzed ([26, 27]; see Supplemental Experimental Procedures available online) 5,484 waggle dances to make a two-year analysis of natural foraging over a mixed urban-rural landscape by three honeybee colonies located at the laboratory across the surrounding 94 km^2 (Figure 1). Because we were only interested in where honeybees indicate profit, and not details about the type of forage, we did not distinguish between dances for nectar and for pollen (See Supplemental Experimental Procedures for more detail). We then used the standard land-type categories from Natural England, a major national organization responsible to the UK government whose purpose is to protect the natural environment, and from Digimap, a web-mapping service from EDINA, the University of Edinburgh-based national data center, to divide up the landscape into seven land types: (1), urban; (2) rural not under any AES; and (3)–(7), rural under one of five AESs by Natural England (see Supplemental Experimental Procedures). These five AESs are Entry Level Stewardship (ELS), Entry plus Higher Level Stewardship, Higher Level Stewardship (HLS), Organic Entry Level Stewardship (OELS), and Organic Entry plus Higher Level Stewardship (Table 1; Figures 3 and S1). Additionally, some areas carry additional notable designations, such as National or Local Nature Reserve status.

Honeybees have evolved exceptional sensitivity to relative energetic reward [14–16]. Forage profit will tend to decrease

*Correspondence: m.couvillon@sussex.ac.uk

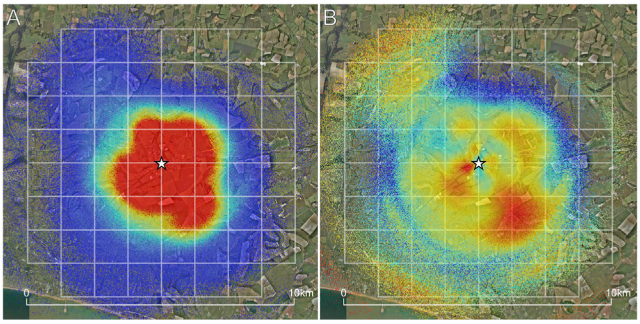

Figure 1. Distribution and Density of Foraging Locations as Determined by Decoding Waggle Dances

Foraging honeybees were kept in three observation hives at the laboratory (white star). Dances are mapped before (A) and after (B) correcting for distance. Color denotes the probability of visitation (A) or residual probability of visitation (B), where no color = no probability visitation, blue = low probability of visitation, and red = high probability of visitation. To correct for spatial nonindependence, our analysis implemented a randomized blocking design of sixty 1250 × 1250 m squares (overlaid white grid; see Supplemental Experimental Procedures). We analyzed honeybee foraging patterns in the gridded area of 94 km^2, chosen to include 99% of the dance vectors.

Table 1. Honeybees Demonstrate a Significantly Positive Preference for Rural Lands under HLS and a Significantly Negative Preference for Rural Lands under OELS

Category of Land Type	Estimate	t Value	p Value
(Intercept)	0.63963	1.400	0.1674
Urban	−0.20886	−1.158	0.2521
Rural: no stewardship	−0.75321	−1.519	0.1347
Rural: Entry Level (ELS)	0.01429	0.079	0.9374
Rural: Entry plus Higher	0.08967	0.356	0.7232
Rural: Higher Level (HLS)	0.38216	2.148	0.0364*
Rural: Organic Entry Level (OELS)	−0.59692	−2.640	0.0109**
Rural: Organic Entry plus Higher	−0.10037	−0.517	0.6077

Land type is a significant factor in honeybee foraging profitability, as shown by dancing (adjusted $R^2 = 0.144$, $F_{7,52} = 2.414$, p = 0.032). Across two years, honeybees danced significantly more for land with HLS (*p = 0.036) and significantly less for land with OELS (**p = 0.011).

with increasing flight distance, which can be seen, as in previous studies [14, 15, 28, 29], by the decrease in dance probability with increasing distance from the hive (Figure 2). Therefore, to evaluate the relative importance of different land types to honeybees, we corrected for distance by adding it as a covariate in the analysis (Figure 1B; see Supplemental Experimental Procedures). This has not been done in any previous study using dance decoding to study honeybee foraging. Additionally, our data on honeybee visitation probability per 25 × 25 m bin (Figure 1) show a strong degree of spatial autocorrelation, where adjacent bins are not statistically independent (see Supplemental Experimental Procedures). This occurs for two reasons. First, the error inherent in the dance [14] means that we visualize honeybee visitation as a probability distribution ([27]; see Supplemental Experimental Procedures). Second, adjacent areas tend to share land-type characteristics. Therefore, we implemented a randomized blocking design (1250 × 1250 m squares; Figures 1, 3, and S2), which is an established method to correct for spatial nonindependence [30]. This block size also corresponds well to the average polygon size of our landscape (1.3 km^2) and allows us sufficient resolution of land-type features. Lastly, because 99% of the dances occurred within 4455 m, we decided to exclude from the analysis any block beyond that range. Ultimately we ended up with 60 blocks, each 1250 × 1250 m (1.56 km^2), covering a total of 93.75 km^2, which we analyzed for honeybee dancing (Figures 1 and 3) in a linear mixed-effect model (see Supplemental Experimental Procedures for details).

The Most Visited Block Contains a National Nature Reserve

The highest ranked block, communicated the most frequently by dancing bees as a profitable area over the two years when distance to the hives is factored out, is 2 km southeast of the laboratory (Figure 3, square labeled "1"). This square includes Castle Hill, a rural land National Nature Reserve under HLS (red land type). We determined block ranks by extracting the best linear unbiased predictors (BLUPs) from a linear mixed-effect model analyzing the probability of visitation against distance and land type but allowing individual block intercepts to vary (Supplemental Experimental Procedures). Importantly, the second highest ranked block also contains HLS land (Figure 3, square labeled "2") and includes the Ditchling Beacon Local Nature Reserve, an area of National Trust land managed by Sussex Wildlife Trust for 34 years to restore chalk grassland.

Honeybees Communicate a Significant Preference for HLS and against OELS

Our results (Figure 3) demonstrate that there is great variation in honeybee foraging in the landscape, with some areas utilized significantly more than others. To examine this more formally, we used a linear model to analyze BLUPs against the presence or absence of the seven categories of landscape. Overall, we found a significant effect of land type (F = 2.414, p = 0.032; Table 1). By looking at the sign of the estimate (positive or negative), we can then determine whether each land-type category is associated with lower or higher visitation than expected, given the distance; this then can be coupled with the p value to assign significance.

We found that blocks with rural lands under ELS, Entry plus Higher, and HLS were visited more than expected (i.e., possessed positive estimates). In contrast, we found that blocks with urban land, rural land not under AES, and rural land under both types of Organic Stewardship (OELS and Organic Entry plus Higher) were visited less than expected (i.e., possessed negative estimates). Of all these results, the two significant effects were found for HLS (significantly positive) and OELS (significantly negative), which means that if blocks contained rural land under HLS, the block was communicated as profitable by dancing bees significantly more than expected (Figure 3; Table 1; p = 0.036), whereas if it contained rural land under OELS, the block was communicated significantly less than expected (Figure 3; Table 1; p = 0.011). HLS is one of the most complex AESs, aiming to deliver "significant environmental benefits to priority areas" [3, 4]. Interestingly, one HLS prescription usually involves the creation and maintenance of long-term set-asides and temporary grasslands, which would allow the growth of forage-rich wildflowers [3, 4]. In contrast, it may be that the practices encouraged under OELS are not specifically beneficial to bees. For example, it is common for lands newly under OELS first to be sown with organic seed mixes of nectar-rich plants, such as clover or bird's-foot trefoil, and second to be regularly mowed within the first 12 months to discourage the growth of nontarget plants [3, 4]. The regular cutting may additionally preclude the nectar-rich plants from blooming, ultimately resulting in

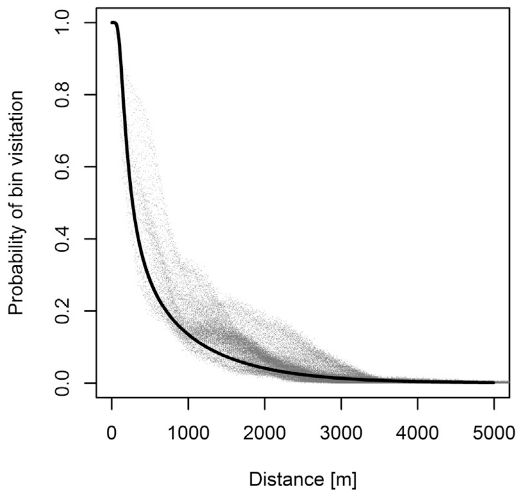

Figure 2. The Probability of Honeybee Visitation Is Inversely Proportional to Distance from Hives

Each gray point is the distance of a 25 × 25 m bin against the probability that it was visited $p_{visited}$ (range: 0–1) during our study (see Supplemental Experimental Procedures). The black line was modeled as logit($p_{visited}$) ~ distance + (1/distance), which we then back-transformed for plotting.

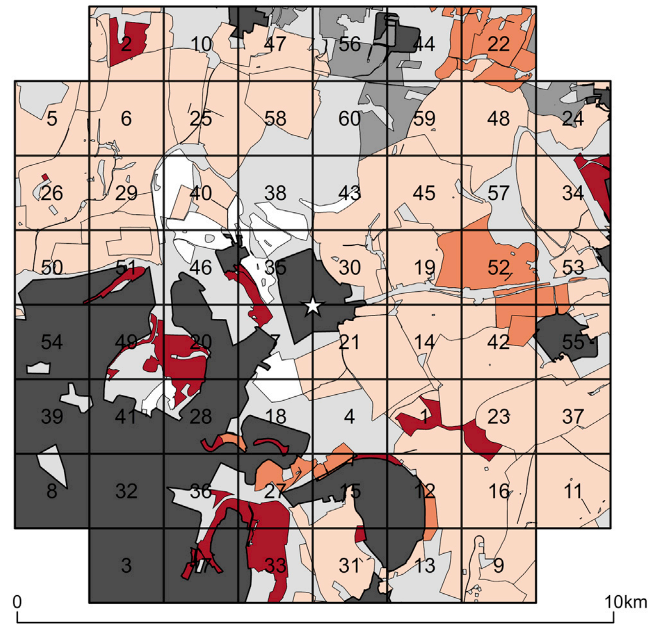

Figure 3. Honeybee Biomonitoring of Landscape Profitability Indicates a Significant Foraging Preference for Rural HLS Land Generally and Castle Hill National Nature Reserve Specifically

Foraging preferences were determined by decoding waggle dances, and the landscape was divided into 60 blocks (1.25 × 1.25 km) across the landscape around the apiary location (center star). The number in each block shows its rank in terms of honeybee foraging when the effect of distance has been removed. Color denotes land type: urban, dark gray; rural not under any AES, light gray; rural under ELS, salmon; rural under ELS + HLS, light pink; rural under HLS, red; rural under OELS, medium gray; rural under OELS + HLS, white. The highest ranked block (labeled "1") contains the Castle Hill National Nature Reserve, which is under HLS. The second highest ranked block ("2") also contains HLS land that includes the local Ditchling Beacon Local Nature Reserve.

fields that, for the first few years, possess very few flowers for forage. Lastly, despite a recent tripling in the number of managed London hives and a general rise in urban beekeeping [31], we did not find evidence that honeybees preferentially visit built-up urban areas in the study landscape. Instead, there was even a slight, nonsignificant trend for bees not to visit urban areas (Table 1, negative estimate for urban).

The Broader Relevance of Honeybee Foraging Data to Evaluate the Landscape, to Other Insect Pollinators, and as Possible Bioindicators

Here we have used a unique pollinator communication behavior to evaluate the rural landscape, which possesses large areas under government-regulated environmental schemes. We have shown generally that land under HLS and specifically a National and Local Nature Reserve are important repositories of forage for honeybees. National Nature Reserves, of which there are 224 around the UK, are specifically managed for the preservation of flora, fauna, and features of interest; additionally, they have recently been threatened by proposed budget cuts [32]. Our data may help demonstrate the importance of maintaining such areas.

The honeybee is only one species of insect, but our dance decoding data show that honeybee foraging has wider relevance. In particular, the two most visited of the 60 blocks in the 94 km^2 survey landscape contained Castle Hill National Nature Reserve and Ditchling Beacon Local Nature Reserve, both known for wildflowers and butterflies [33]. This shows that honeybee dance decoding can locate important areas that support other species, most likely because the honeybee is a generalist forager and collects food where other insect pollinators also forage [34].

Although our land-type categories (urban, rural, and rural land under improvement schemes) are broad and generally found in Western Europe (e.g., agri-environment schemes) and the United States (e.g., the USDA's Conservation Stewardship Program and Environmental Quality Incentives Program), it is important to remember that our study was set in one location. It is possible that honeybees may display different foraging preferences in differently structured landscapes. For example, other urban landscapes may be more attractive, and other rural non-AES areas may be naturally more productive, which will certainly impact foraging preferences [35]. Additionally, AES categories and prescriptions may also vary with country. It would be interesting for future research to evaluate honeybee foraging preferences in other locations and to compare those data with our results here to see what areas honeybees indicate as important in other settings.

Biomonitoring via the use of "indicator" species or groups is well known in environmental science, where, for example, lichen presence has been used to indicate "atmospheric health." Our results here demonstrate that honeybee dances indicate "landscape health," applicable to a wide range of pollinators. By using three honeybee hives, we made a broad analysis over 94 km^2. Imagine the time, manpower, and consequent cost required to survey such an area on foot, including monitoring nectar sources, their quality and quantity, and the number of flower-visiting insects competing for them, and doing so over the 16 months of a two-year foraging season. Instead, we have allowed the honeybees to survey the landscape, integrate all relevant costs, and perform their dance communications, which therefore provide cost-effective, integrated, and biologically relevant information regarding landscape quality for insect pollinators. The waggle dance is therefore more than just a honeybee behavior: it is a powerful tool for ecology and conservation, providing unique information that may help to evaluate landscapes and guide human efforts to sustain a more wildlife-friendly world.

Supplemental Information

Supplemental Information includes two figures and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.03.072.

Author Contributions

M.J.C. and F.L.W.R. designed the experiment. M.J.C. oversaw data collection, performed analyses, and wrote the paper. R.S. performed mathematical and statistical analysis. F.L.W.R. contributed to all stages. All authors commented on the manuscript and take full responsibility for its content.

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