



Foraging of honey bees in agricultural landscapes with changing patterns of flower resources

Svenja Bänsch^{a,b,*}, Teja Tschardt^a, Francis L.W. Ratnieks^c, Stephan Härtel^d, Catrin Westphal^b

^a Agroecology, Department Crop Sciences, University of Göttingen, Göttingen, Germany

^b Functional Agrobiodiversity, Department Crop Sciences, University of Göttingen, Göttingen, Germany

^c Laboratory of Apiculture and Social Insects (LASI), School of Life Sciences, University of Sussex, Brighton, UK

^d Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Würzburg, Germany

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ABSTRACT

The demand for crop pollination is increasing and honey bees are frequently used, in particular as wild pollinators are in decline. Temporal and spatial variation of flower resources affects foraging decisions of wild and honey bees. To optimise crop pollination management a better understanding of potential competition for pollinators in mass- and minor-flowering crops is needed.

We combined waggle dance decoding, pollen load analysis and field surveys to identify the habitat preferences and pollen use of honey bees in response to spatio-temporal changes in resource availability. Observation hives were placed on the edge of eleven fields of blooming strawberries (mean 2.24 ha) located in landscapes with different amounts of oilseed rape (OSR), semi-natural habitats (SNH) and apple trees in Germany. In addition, we surveyed honey bees and wild bees in strawberry fields.

Honey bee dances more often indicated strawberry, OSR fields and SNH than expected given their landscape-wide areas. Honey bees collected on average 7.9 % strawberry, 49.0 % OSR, 30.2 % *Pyrus* type (e.g. apple) and 12.9 % other pollen types. The mean honey bee foraging distance was 740 m, and decreased with OSR availability. In the observation hives, dances for strawberry fields were not directly affected by OSR availability or SNH land cover. But large amounts of OSR reduced overall honey bee and bumble bee abundance in strawberry fields, while solitary bees were unaffected. Bumble bees were most abundant in strawberry fields (54.1%) and together with solitary bees (19.7%) they represented about 75.0% of the observed bees.

Minor-flowering strawberry fields represent a preferred resource for honey bees, especially for small colonies as indicated by decoding of waggle dances. However, the availability of more attractive OSR and local strawberry flower cover moderates the abundance of social bees (honey bees and bumble bees) in strawberry fields while other wild bees were less affected. Hence, we conclude that wild bee conservation plays a major role for strawberry pollination. If pollination services by solitary bees are limited, small honey bee hives can be used scrupulously to supplement pollination services in strawberries.

1. Introduction

Insect pollination can increase the yield and quality of many crops and wild plants worldwide (Klein et al., 2007; Klatt et al., 2013). The economic value of pollination services in agricultural production is estimated to be 153–577 billion US\$ (Gallai et al., 2009; Lautenbach et al., 2012). As global fruit production intensifies, the demand for pollination is increasing (Aizen and Harder, 2009). However, wild pollinators are currently threatened and in decline, due to multiple stressors associated with agricultural intensification, such as fragmentation of flower-rich semi-natural habitats (SNH) and homogenous

cropping systems (Potts et al., 2010, 2016; Kovács-Hostyánszki et al., 2017). The resource availability of entomophilous crops and flowers in SNH habitats can be limited to certain time periods. A temporal shortage of foraging resources is likely to decrease population dynamics of wild and honey bees in agricultural landscapes (Schellhorn et al., 2015; Wintermantel et al., 2019).

A better understanding of the foraging ecology of honey bees can contribute to maintaining crop pollination services. The honey bee, *Apis mellifera* L., is the most important pollinator in crop production and is relevant globally (Aizen and Harder, 2009; Kleijn et al., 2015). Worker honey bee collect pollen and nectar from a great variety of plant species

* Corresponding author at: Grisebachstraße 6, 37077, Göttingen, Germany.

E-mail address: Svenja.baensch@agr.uni-goettingen.de (S. Bänsch).

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(polylectic) and are known to collect pollen with high flower constancy, which can be linked to improved pollination efficiency (Montgomery, 2009). However, the spatial ecology of honey bee foraging in relation to spatio-temporal shifts in resource availability at the landscape scale is not well understood. The waggle dance honey bees use to communicate rewarding resources is a unique way of investigating foraging at a landscape level, and can give information about the distance and direction of the most profitable nectar and pollen resources being visited (Von Frisch, 1967; Couvillon et al., 2012a). Decoding the dances can help to understand the foraging of honey bees with respect to seasonal changes in resource availability and in target crops (Danner et al., 2016; Balfour and Ratnieks, 2017; Garbuzov et al., 2015). Pollen foraging can also be determined by identifying the abundance of collected plant species in pollen loads (Danner et al., 2016; Balfour and Ratnieks, 2017; Marzinzig et al., 2018; Garbuzov et al., 2015). Recently, it has been shown that honey bees with an intact dance communication were able to collect a greater pollen diversity compared to colonies with experimentally disturbed communication (Nürnberg et al., 2019).

Honey bees prefer to forage in agricultural landscapes on flowers in SNH, on flowering woody structures, weeds and (mass-) flowering crops such as oilseed rape (OSR, *Brassica napus* L.) (Rollin et al., 2013; Requier et al., 2015; Danner et al., 2016; Sponsler et al., 2017). Routinely, they forage in distances of 1.5 km, but can also forage on resources in distances up to 12–14 km (Visscher and Seeley, 1982; Beekman and Ratnieks, 2000; Steffan-Dewenter and Kuhn, 2003). As honey bees tend to optimise their foraging (Seeley, 1995) the availability of resources and landscape structures can affect their foraging behaviour (Steffan-Dewenter et al., 2002; Garbuzov et al., 2015; Danner et al., 2016). The availability of mass resources can be linked to shorter foraging distances (e.g., Danner et al., 2016). Foraging distance in spring, when mass resources such as OSR and flowers in SNH are in bloom, is likely less than 1 km (Beekman and Ratnieks, 2000; Couvillon et al., 2014; Danner et al., 2016; Balfour and Ratnieks, 2017; Danner et al., 2017).

These previous studies show that improved understanding of the spatial foraging pattern of honey bees in response to temporal changes of resource availability at the landscape scale is relevant to the use of honey bees for crop pollination. In this study we investigated the pollination of strawberry, a fruit crop which often flowers at the same time as mass-flowering OSR, by honey bees and wild bees. Previous studies found that honey bee abundance in strawberry fields with minor rewards can be negatively affected by co-flowering mass resources such as OSR or apple (Bänisch et al., unpublished data; Grab et al., 2017). Our study combined three methodologies: 1) waggle dance decoding from small hives at the edge of strawberry fields; 2) analysis of pollen loads of honey bees collected in pollen traps at the hives; 3) surveys of bees foraging in strawberry fields. The data collected were used to address three questions: 1) What land use types with pollen and nectar-providing plant species are most used by honey bees in the agricultural landscape? 2) Do alternative resources (e.g. OSR and SNH) affect honey bee foraging distance? 3) Does the availability of these alternative resources affect the proportion of waggle dances for strawberry fields, the proportion of strawberry pollen collected, and bee abundance in strawberry fields?

2. Methods

2.1. Study fields and study landscapes

We studied eleven conventionally managed strawberry fields in central Germany in the regions surrounding the cities of Kassel and Göttingen in 2017 (Fig. 1). Most strawberry fields were managed for harvesting via public self-pick harvesting and usually about three varieties of different peak flowering periods were grown to extend the harvesting season. Mean field size was 2.24 ha (± 1.02 SE; range 0.92–3.6 ha). The study fields were surrounded by a landscape mosaic

consisting of arable crop fields, fragments of SNH, forests and urban area.

To identify the preferred land use types of honey bees, we created digital maps of the land cover types of the study landscapes surrounding our study fields in 750 m radii using a geographic information system (ESRI ArcGIS, Version 10.3.1). We focused on 750 m since the observed mean foraging distances of honey bees were rather short during the study period ($740 \text{ m} \pm 26 \text{ SE}$). We calculated the proportion of land cover (%) within study landscapes of following land use types: strawberry fields (only one study field per study landscape; $1.3 \% \pm 0.2$), OSR fields ($8.6 \% \pm 2.4$), SNH ($6.7 \% \pm 0.9$), cropland ($66.4 \% \pm 4.0$), forest ($0.9 \% \pm 0.4$) and urban area ($16.2 \% \pm 5.0$) (Table S1). Agricultural field data (e.g. cropping type) are based on InVeKos data (database of agricultural cropping; <https://www.zi-daten.de/>) provided by the German states Lower Saxony (Landwirtschaftskammer Niedersachsen, 2017) and Hesse (Landesbetrieb Landwirtschaft Hessen, 2017). The land use category ‘cropland’ comprises the entire agricultural landscape matrix, i.e. crop fields (mainly non-flowering annual crops, such as cereals or sugar beets), field margins and country lanes. Scattered trees (including fruit trees, such as apple) along roads and country lanes have not been mapped separately. Flowering crops (i.e. strawberry and OSR fields) have been treated as separate category. SNH include non-cultivated landscape elements, such as hedges, meadows, shrub lands and meadow orchards with fruit trees, like apple, that provide potential foraging resources for honey bees and nesting for wild bees. Cropland and urban area can provide various and attractive resource patches (e.g. flowering weeds and homegarden plants) but we were unable to map them in detail due to an insufficient resolution of maps and the large amount and diversity of resource types.

As both the area of OSR fields in the landscape and the flower cover within OSR fields can determine the abundance of OSR nectar and pollen resources, we calculated an index for OSR availability. OSR availability is the product of OSR land cover (ha) within a radius of 750 m and the OSR flower cover estimated in the nearest OSR field to the hive along a transect of $50 \times 4 \text{ m}$. The distance to the nearest OSR field was correlated with the OSR land cover within a radius of 750 m ($r = -0.8$, $p = 0.0032$). The more OSR land cover within the landscape surveys the closer was the nearest OSR field. All OSR fields had a relatively uniform germination and performance in the study landscapes. The average distance to SNH was $71.5 \text{ m} \pm 20.3$ (range 10–193 m) but land cover and distance was not correlated.

2.2. Observation hives

To study the waggle dance, we used two-frame observation hives (Supplementary information Fig. S1), each with approximately 4,000 worker bees and a queen bee of same age (*A. mellifera carnica* Pollmann, provided by W. Seip Biozentrum GmbH & Co. KG, Germany). The observation hives were modified so that returning bees were led to one site of the comb first, where we did video recordings following Danner et al. (2016). One hive per study field was positioned at the edge of the strawberry field on the 27th or 28th April 2017. Additional food (sugar solution) was provided if needed.

2.3. Waggle dance decoding

To observe the waggle dances we made video recordings on four recording days during the strawberry and OSR flowering period from the 30th April until 5th June 2017, using a camcorder (Sony HDR CX240E). For the recording dates we chose only days with low wind speed, no rain and a minimum temperature of 14°C . The recording times were equally distributed to morning and afternoon hours (9 a.m. – 5 p.m.) to account for pollen and nectar availability of different plant species throughout the day.

Each video recording lasted 90 min and we decoded, if possible, 20 dances per record (mean $18.07 \pm 0.37 \text{ SE}$). To differentiate between



Fig. 1. Location of study fields (red circles) in the surroundings of Göttingen and Kassel, central Germany (a); 1:700,000. Basemap source: ESRI basemap (Bing).

potential nectar and pollen foragers, we noted whether dancing bees carried visible pollen or not. Bees without pollen loads were presumably nectar forager. After two rounds of video recordings we rotated the hives once between the study fields to reduce potential effects of intrinsic differences among hives. In addition, we accounted for potential hive effects within our statistical analysis.

We decoded waggle dances following a protocol from Couvillon et al. (2012b). For each waggle dance we measured the angle relative to vertical, which then can be converted into the direction by adding the azimuth of the sun at the time of the dance (macro by W. Towne, Kutztown University, Pennsylvania, USA). The time of the waggle run can be translated into the foraging distance, but short dance durations can result in low or even negative values, based on the calibration curve, especially for values that would result in distances < 100 m (Schürch et al., 2013). Those dances were set to 100 m, as honey bees (*A. mellifera carnica* P.) typically communicate resources in distances below 100 m by round dances and not waggle dances (Von Frisch, 1967). As round dances point to a resource close to the hive, we counted them as visits in strawberry fields that were the most rewarding resource in the close surroundings of the hives (< 100 m). In three out of the eleven landscapes single fruit trees or bushes may have been also flowering close to the hives, so we cannot entirely preclude that bees have performed the round dance for these resources.

To identify the visited land use types indicated by the waggle dance we combined the spatial information (distance and direction) with our digitalised land cover maps. We then counted the number of dances, which were assigned to certain mapped land cover types (i.e. strawberry field, OSR fields, SNH, cropland, forest and urban area, Supplementary information Fig. S2). Dances that were assigned to streets (25 dances) were excluded from the data set.

2.4. Pollen analysis

At each observation date, we collected pollen loads from homecoming bees for ten minutes (or at least from 10 bees) directly after the

waggle dance recordings to analyse exploited pollen resources. Pollen samples were pooled per hive and date, and stirred with 500–1000 μ l water, depending on the sample size, to homogenise them. A drop of each sample was fixed on microscopic slides with glycerine gelatine. Following the guidelines of pollen identification in honey samples (Dustmann, 2006), 500 pollen grains per sample were identified and counted by a pollen identification expert (S. Böhrs, Mellisopal Pollenanalytik, Germany). Pollen belonging to the *Pyrus* type can be mainly assigned to pome fruits, such as apples (*Malus* sp.) and pears (*Pyrus* sp.). In our study region most common fruit trees are apple trees that flower usually until beginning/ mid of of May which overlaps with the OSR bloom for a short period of time.

2.5. Surveys of bees in strawberry fields

We conducted transect walks in strawberry fields during the video recordings and chose rows with the highest strawberry flower cover for transects (50 m \times 4 m). Flower cover was quantified by counting open flowers along two meters of a representative strawberry row within the transect walk. All flower-visiting bees were caught with an insect net and either identified in the field (particularly honey bees, common bumble bees and characteristic solitary bees) or killed with ethylacetate and identified by F. Creutzburg (Jenisect, Jena). We assigned the bees to functional groups, namely honey bees, bumble bees and solitary bees, according to their sociality, level of domestication and foraging behaviour (e.g. foraging ranges, see also Rollin et al., 2013).

2.6. Data analysis

2.6.1. Identification of preferred foraging habitats

We assume that in a homogeneously attractive landscape the proportion of land cover of different land use types (strawberry, OSR, SNH, cropland, forest and urban) should equal the frequency of observed dances pointing to these. We identified preferred foraging habitats by comparing the frequency of observed dances versus the proportion of

expected dances (equals land cover) for certain land uses using Chi² Test. Habitats with higher frequencies of observed dances than expected were classified as preferred foraging habitats. Standard residuals were extracted to explain the strength of difference between observed and expected values.

2.6.2. Effects of landscape-wide resource availability of foraging distances

We tested how OSR availability and SNH land cover affected the foraging distances using linear mixed effect models (function 'lmer', package 'lme4', (Bates et al., 2014)). Round dances were excluded from this analysis since they do not indicate a quantifiable foraging distance. The foraging distance was square root transformed to achieve a random distribution of the residuals and homogeneity of variances. We included the observation round nested in landscape and hive as crossed random terms in the models.

We first fitted a global model including the following explanatory variables: OSR availability, SNH land cover, pollen collection (pollen present/absent), and their two-way interactions. All explanatory variables were checked for potential correlations. We found only little if any correlation ($-0.3 < r < 0.3$, (Hinkle et al., 2003)). Continuous explanatory variables were scaled to a mean of zero and a standard deviation of 1.

We employed the multimodel inference approach (Burnham and Anderson, 2002) to select the best fitting models. Models were ranked by the second order Akaike Information Criterion (AICc) and we used the Akaike weight (w_i) to estimate the probability of the individual models to have the best fit across all models (Burnham and Anderson, 2004). All models within delta AICc ($\Delta AICc$) < 2 from the best fitting model were considered to have substantial empirical support and are reported together with the null model (model which is not taking any explanatory variables into account) and the global model (Supplementary information Table S2). Appropriateness of model assumptions was assessed by plotting residuals vs. fitted values. The relative importance of each explanatory variable was assessed using the sum of Akaike weights (Σw_i) over all candidate models that included the respective variables (function 'importance', package 'MuMin', (Barton, 2018)). We considered $\Sigma w_i > 0.2$ to explain effects on our response variables.

2.6.3. Exploitation of strawberry fields

To analyse whether OSR availability and the proportion of SNH land cover alter the proportion of dances pointing to the strawberry field and the proportion of collected strawberry pollen, we used generalised linear mixed effects models with binomial distribution (function 'glmmTMB', package 'glmmTMB', (Brooks et al., 2017; Bolker, 2018)) for both response variables. OSR availability, SNH land cover and the interaction between both were included as explanatory variables and region and hive as crossed random terms. We accounted for overdispersion by observation level random effects in both models (Harrison, 2015). Again, we used the multimodel inference approach to identify the best fitting models and the relative importance of each explanatory variable as described above.

2.6.4. Bee abundance in strawberry fields

To investigate the effects of OSR availability, SNH land cover and local strawberry flower cover on bee abundances we grouped the bees into honey bees (HB), bumble bees (BB) and other mostly solitary bees (SB). Models were fitted for each functional group with generalised linear mixed effect models using the 'glmmTMB' package (function 'glmmTMB', (Brooks et al., 2017)). The abundance of honey bees followed a Poisson distribution and we accounted for overdispersion in bumble bee and solitary bee abundance with negative binomial distribution. Again, we used the multimodel inference approach to choose the best fitting models and to identify the relative importance of explanatory variables as described above.

All statistical analyses were performed with the software R version

3.5.0 (R Core Team, 2016).

3. Results

In total we observed 784 dances (768 waggle dances and 16 round dances). Almost half of dancing bees (45.9 %) carried visible pollen loads.

3.1. Preferred foraging habitats

We found that 42 of 784 dances (5.4 % of all dances observed) pointed to the neighbouring strawberry fields, including both waggle dances and round dances. About half of the dancing bees (20 out of 42) carried visible pollen. Another 95 dances pointed at OSR fields (12.1 %) and only 28 bees carried visible pollen loads. We found 59 dances (7.5 %) pointing to SNH and most bees (37 bees) carried visible pollen loads. The majority of dances pointed to unspecified cropland (60.0 % of all dances observed), 11.0 % dances pointed to urban area and 4.1 % at forest.

The observed frequencies of dances were higher than expected (based on the land cover of respective land use types) for the land use types strawberry, OSR, SNH and forest while it was lower for urban area and cropland ($\chi^2 = 248.82$, $df = 5$, $p < 0.001$, Fig. 2).

Our pollen analysis showed that strawberry pollen amounted to $7.9 \% \pm 2.7$ SE on average in the pollen samples (up to 85.0 % in individual samples). OSR was the most dominant pollen type that reached proportions of up to 100.0 % (mean $49.0 \% \pm 5.7$). Another major pollen resource was identified as *Pyrus L.* type (mean $30.2 \% \pm 5.9$). *Pyrus* includes all pome types, but we expect apple pollen to represent the largest amount because apple bloomed at a similar time and is cropped frequently in our landscapes in orchards, old meadows, along roadsides, and in gardens. The remaining pollen was collected to a small extent from plants such as *Salix L.*, *Rubus L.* and *Taraxacum*. In general, pollen diversity was low with only one to five different pollen types per sample.

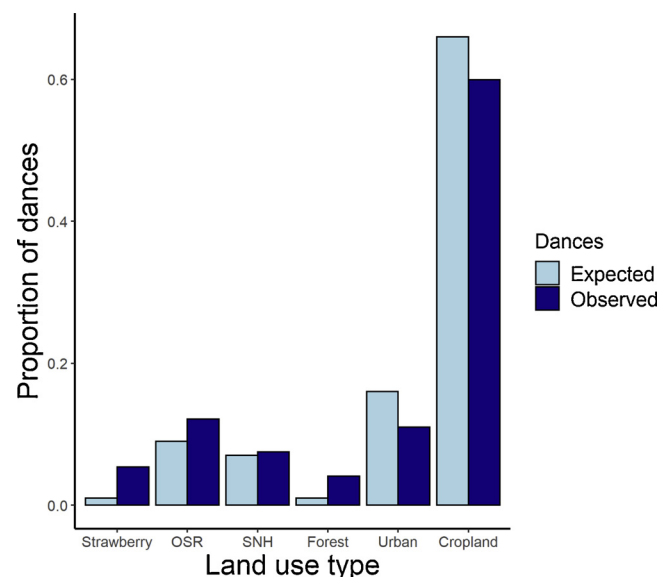


Fig. 2. Expected proportions of dances (light blue) versus the observed proportions of dances (dark blue) for the dominant land use types ($n = 784$). The observed proportion of dances is higher for strawberry, oilseed rape (OSR), semi-natural habitats (SNH) and forest compared to the expected proportion. While the proportion of expected dances is higher for urban areas and cropland than observed. Residuals according to Pearson's Chi Square test are for strawberry 12.26, for OSR 3.05, for SNH 0.58, for forest 8.67, for urban area -3.84 and for cropland -3.58 .

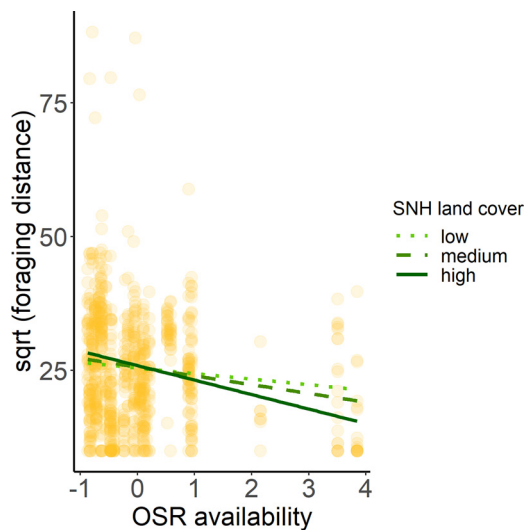


Fig. 3. Interactive effects of OSR availability and SNH land cover on the foraging distance of honey bees ($n = 743$). The foraging distance of honey bees decrease with increasing OSR availability, particularly when SNH land cover is high. Foraging distance is shown on square root scale in response to scaled OSR availability (scaled to a mean of zero and standard deviation of 1) as fitted in the model and data points are jittered. Regression lines are obtained from mixed model estimates and are predicted for low, medium and high SNH land cover (i.e. 10, 50, 90- percentile of observed data).

3.2. Effects of landscape-wide resource availability on foraging distances

The foraging distance estimated by the duration of waggle dances of honey bees was on average $740 \text{ m} \pm 26 \text{ SE}$, range 100–7783 m. The foraging distance of honey bees with pollen was on average $697 \text{ m} (\pm 40 \text{ SE})$ and differed only slightly from the foraging distance of bees without visible pollen $775 \text{ m} (\pm 35 \text{ SE})$. The effects of OSR availability, SNH land cover, and pollen collection on the foraging distance were explained by several models with empirical support ($\Delta\text{AICc} < 2$, Supplementary information Table S2a). In the best fitting model all main effects and an interaction between OSR availability and SNH land cover were included (Supplementary information Table S2a). Pollen resource use was the most important explanatory variables indicated by the high $\Sigma\text{wi} = 0.94$, followed by OSR ($\Sigma\text{wi} = 0.93$), followed by SNH land cover ($\Sigma\text{wi} = 0.74$) and an interaction between OSR availability and SNH land cover ($\Sigma\text{wi} = 0.47$, Supplementary information Table S3). The foraging distance of honey bees decreased when OSR availability increased and SNH land cover was high (Fig. 3). While the main effect of OSR availability was negatively correlated with foraging distances (e.g. short foraging distances), the main effect of SNH land cover was positively correlated with foraging distances (e.g. increasing foraging distance, estimates can be found in Supplementary information Table S4a). Further, marginal interactive effects of OSR availability and pollen use ($\Sigma\text{wi} = 0.42$) and of SNH land cover and pollen use ($\Sigma\text{wi} = 0.35$) were found in the second and third best fitting models. The interactive effects showed that foragers without visible pollen loads showed stronger responses to OSR availability and SNH land cover (Supplementary information Fig. S3a–b). Forager without visible pollen loads indicated longer foraging distances when SNH land cover increased and shorter foraging distances when OSR availability increased compared to forager with visible pollen loads.

3.3. Exploitation of strawberry fields

Neither was the frequency of dances pointing to strawberry fields nor the proportion of strawberry pollen in the pollen samples related to OSR availability or SNH land cover. The best fitting models were either the null model or differed not substantially from it ($\Delta\text{AICc} < 2$)

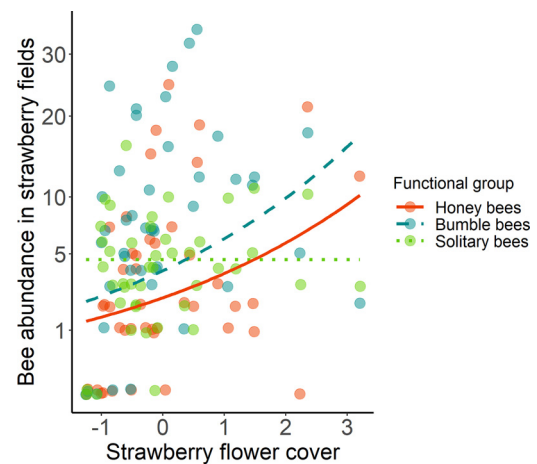


Fig. 4. Effects of strawberry flower cover (%) on the number of bees per transect in strawberry fields (bee abundance) for each functional group. The number of honey bees and bumble bees per transect in the strawberry fields is enhanced with increasing strawberry flower cover while solitary bee abundance was not affected. Strawberry flower cover is scaled (to a mean of zero and standard deviation of 1) as fitted in the model and data points are jittered. Regression lines are obtained from mixed effect model estimates.

(Supplementary information Table S2b–c).

3.4. Bee abundance in strawberry fields

We recorded in total 883 pollinator-flower interactions in strawberry fields, 218 bees belong to honey bees, 450 bees to the genus *Bombus* (mainly *B. terrestris* L.), 164 individuals were assigned to solitary bees and 51 bees were excluded as they were neither caught or identified (species list can be found in Supplementary information Table S5). OSR availability and local strawberry flower cover determined the honey bee and bumble bee abundances in the strawberry fields (Supplementary information Table S2d). Strawberry flower cover was the only predictor variable in the best fitting model and the most important predictor variable for both functional groups (Σwi for HB: 0.82, for BB: 0.81, Supplementary information Table S6). Increasing strawberry flower cover correlated positively with social bee abundances in the field (Fig. 4). In contrast, increasing OSR availability, which was included in the second best fitting model, correlated negatively with social bee abundances, however the effect was only of minor importance (Σwi for HB: 0.37, BB: 0.35, Supplementary information Table S4b and Fig. S4). SNH land cover was not included within the best fitting models for social bees. We found no effect of OSR availability, SNH land cover and strawberry flower cover on solitary bee abundance in the strawberry field (Supplementary information Table S2d).

4. Discussion

Our study showed that OSR fields, SNH and strawberry fields were the preferred foraging land use types of honey bees, while cropland and urban area were less visited. Increasing both OSR availability and the proportion of SNH land cover shortened the foraging distance and therefore should have benefited the energy balance of honey bees. However, we found no effects of OSR availability and SNH land cover on the strawberry foraging behaviour of honey bees. Bumble bees, together with solitary bees, represented the majority of bees in the strawberry fields.

4.1. Preferred foraging habitats

OSR and SNH were similarly preferred by honey bees, while [Danner](#)

et al. (2016) found even greater preference for SNH. This may depend largely on the quantity and quality of flowering resources in SNH (Kleijn and van Langevelde, 2006). A great number of dances were performed for cropland in general, as this kind of habitat can provide flowering weed patches, woody and herbaceous structures (Requier et al., 2015). A great frequency of dances has been observed for forest as well but many dances were performed in one landscape at one time suggesting a mass-flowering effect that might be caused by flowering maples (de Vere et al., 2017). Although only a small frequency of dances pointed to the neighbouring strawberry field it was still more preferred than OSR and SNH when taking the land cover into account. The strawberry field is only a very small fraction within our study landscapes, but bees prefer to forage close to their hives (Seeley, 1995). Hence, the distance to the hive can also affect the attractiveness of a resource and strawberry pollination may benefit from the close distance to the hives. However, important flower resources such as OSR fields and SNH were easily accessible to our honey bee hives as well. The average distance to the next resource patches were rather small (for OSR 323 m and for SNH 72 m). Moreover, with increasing availability of OSR the distance to the next OSR field declined. Besides the distance to potential foraging resources, the attractiveness of a habitat can also depend on flower availability since honey bees are attracted by mass-flowering resources (Rollin et al., 2013) but they also rely on diverse flower resources to fulfil their foraging requirements (Requier et al., 2015; Hendriksma and Shafir, 2016).

Analyses of pollen loads revealed that bees have used OSR as their main pollen resource, supporting previous studies (Rader et al., 2009; Danner et al., 2017), but contrasting with studies that found only limited pollen foraging on OSR (Garbuzov et al., 2015). The second most abundant pollen was apple. Apple trees are common in agricultural landscapes in our region as well as in urban areas and have been shown to be highly attractive for honey bees (Grab et al., 2017). The importance of small flowering patches and single flowering trees in urban area and cropland might be underestimated with waggle dance analysis as it was not possible to map all minor patches due to dance inaccuracy. In addition, honey bees forage rather for the most profitable resources (Donaldson-Matasci and Dornhaus, 2012; Nürnberger et al., 2019).

4.2. Effects of landscape-wide resource availability on foraging distances

OSR availability and SNH land cover moderated the foraging distance of honey bees. Our results suggest that foraging distances can be shortened due to high resource availability, in particular in OSR fields, which might increase colony fitness (Requier et al., 2015; Danner et al., 2016). The interactive effect of OSR availability and SNH suggested by our results may be of minor significance, as the effect size is rather small and the variability increased with high SNH land cover.

In support of the results of previous studies, we found evidence that the foraging distance is shorter when pollen is collected (Danner et al., 2016; Balfour and Ratnieks, 2017). Honey bees carrying pollen may require more energy since foraging flights take longer when pollen is collected (Winston, 1991). Thus, they might aim to shorten their flight distance. In contrast to Danner et al. (2016), who found that pollen foraging distance decreased when SNH were close to the study hives, we found that a high SNH land cover tends to increase the foraging distance, particularly of nectar foragers. The importance of SNH for foraging bees can be highly variable due to different plant communities in the SNH and due to temporal shifts in flowering phenology. Semi-natural habitats in our landscapes were, for example, hedges with spring-flowering bushes, such as hawthorn (*Crataegus* sp.) but also extensively managed meadows with different plant species communities. The probability of dancing can be further affected by pollen quality (Waddington et al., 1998), which we did not account for in our study. Nevertheless, SNH was especially important as pollen source habitat in our study since about 75.0 % of bees indicating visitation of SNH

carried visible pollen loads.

4.3. Exploitation of strawberry fields and implications for strawberry pollination management

Surprisingly, we did not find direct effects of OSR availability and SNH land cover on the frequency of dances pointing at strawberry fields or on the proportion of collected strawberry pollen in pollen loads but on the abundance of honey bees in the strawberry fields. Since only a small frequency of dances pointed at the adjacent strawberry field and strawberry pollen collection was minor, the dataset might not be sufficient to make profound statements on the effects of co-flowering resources on target crop foraging. A larger dataset would presumably help to disentangle those effects.

In terms of pollination management strategies, what does it mean that only 5.4 % of active forager (about 30.0 %) from a small hive (around 4,000 bees in our study) indicate the strawberry field as valuable resource? Many flowers can still be visited, as 5.4 % of the foragers means about 200 honey bees and one honey bee visits about 7.45 flowers per minute in strawberry crops (Albano et al., 2009). However, those calculations likely underestimate the actual number of foragers, since the majority of foragers is not recruited by waggle dances but rather visits known resources within the close surrounding of the hives. In addition, the probability of recruitment is lower, the closer the flower resource is. In particular, small colonies, that we had in our study, tend to visit adjacent resources frequently (Boecking and Kreipe, 2013). Our results are more in favour of nuclei hives (i.e. small colonies built by beekeepers for breeding and to prevent swarming) than for large commercial bee hives. Hence, one small honey bee hive placed at the edge of a field may significantly contribute to the pollination of strawberries.

4.4. Bee abundance in strawberry fields

Like Connelly et al. (2015), we found that *Bombus* species were the most dominant group in strawberry fields (54.1 %). Together with solitary bees (19.7 %), they represent about 75 % of the bee community in strawberry fields. Honey bees made up only 26.2 % which is in line with previous studies in strawberry fields in the same regions (28.0–33.9 %) (Klatt et al., 2013; Wietzke et al., 2018), but contrasts Grab et al. (2017) (1.3 %). While social bee abundance in strawberry fields decreased with low strawberry flower cover, solitary bees visited the strawberry field independently of local flower cover in the fields. Since almost all honey bees in Germany are managed by beekeepers, their abundance depends strongly on beekeeping activities in the surrounding landscapes. Moreover, honey bee but also bumble bee abundance in strawberry fields can be negatively impacted by mass-flowering events such as OSR flowering, supporting previous findings of competition between minor and mass-flowering crops (Bänisch et al. unpublished data; Grab et al., 2017). Contrarily the abundance of solitary bees was not affected by mass-flowering resources and even facilitated in previous studies (Bänisch et al. unpublished data). Hence, to assure pollination services in minor-flowering crops it is vital to sustain and promote wild pollinators which are often even more efficient pollinators than honey bees, while managed pollinator may still add to crop pollination (Winfree et al., 2008; Garibaldi et al., 2013).

5. Conclusions

Our study shows that landscape-wide mass-flowering resources can influence the foraging distance of honey bees. They have shorter foraging distances with high OSR availability and thus, visited highly rewarding OSR resources nearby more frequently. Interestingly, neither strawberry pollen collection nor the waggle dances towards strawberry fields were negatively affected by high OSR availability indicating a constant exploitation of the fields by the observation hives.

Nevertheless, the overall abundance of honey bees (and bumble bees) in strawberry fields decreased with high OSR availability and low local flower cover in strawberry fields whereas solitary bees were less affected. Hence, the conservation of wild bees and their pollination services plays a major role for strawberry pollination. As solitary wild bees are not strongly influenced by the local flower cover in the fields and mass-flowering crop availability at landscape scale, priority should be given to restore and sustain their pollination services for strawberries and other minor-flowering crops. Managed pollinators can be used scrupulously if natural pollination services are limited. In this case, particularly small honey bee hives with small population sizes appear to be a promising tool for minor crop pollination services since their foraging was rather unaffected by mass-flowering OSR. Otherwise minor-flowering crops may compete with mass-flowering resources such as OSR in the surrounding landscapes.

Authors contribution

SB, CW and TT conceived the study and designed the experiment. SB conducted the field work and together with CW the statistical analysis. SH gave advice on the experimental design, FR on processing of the data and CW, TT and FR on the structure of the first draft. SB wrote the first draft of the manuscript and revised it. CW, TT and FR greatly contributed to the revisions of the manuscript. All authors contributed to the writing of the manuscript and gave final approval for publication.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2019.106792>.

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