Pollen preferences of the honey bee (*Apis mellifera*)

A study in which pollen sources honey bees prefer in spring and how to locate them in the landscape

Photo: By Yoko Luise Dupont. My partner, Annika, to the left, and myself.

Bachelor's project in Biology

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June 2018

Preface

The European Food Safety Authority (EFSA) is EU's food safety agency, and among other things they monitor the decline in honey bees. As honey bees are important for the environment as well as the food industry, EFSA financed a project called "Research project on field data collection for honey bee colony model evaluation". For this project, AU were chosen to perform several experiments to investigate the different stressors for honey bees, such as pesticides, diseases, farming and so forth, to see how these affect the honey bees and to what extent they add to the declining numbers of honey bees worldwide. To contribute, we established a pilot study to determine whether or not waggle dances can be used as an indicator of where honey bees forage, as well as what this tells us about their foraging in general.

All preparatory work and field work was done in cooperation with my partner, Annika Skardsa Jeppesen. This includes testing of observation hive setup, recordings of honey bee waggle dance, collection of honey bees and of pollen, mapping of floral resources in the surrounding landscape, and decoding of waggle dances on videos. Later on, we divided the assignment in two, where Annika focused on the waggle dance and the related uncertainties[1], and I focused on the pollen data and mapping of the landscape.

[1] Jeppesen, A. S. (2018). The honey bee waggle dance: A study in how to measure waggle dance simply and the waggle dance's importance for the honey bees' (*Apis mellifera*) behavior in relation to foraging. Bachelor report, Aarhus University.

Abstract

Honey bees (*Apis mellifera*) are declining in numbers worldwide. Since they are important both economically and ecologically, it is crucial that we learn more about honey bees' wellbeing. The aim of this study was to investigate which pollen sources are the most important pollen sources for honey bees in spring. For this purpose, pollen data and mapping of the landscape around the observation hive were used. Both were compared to decoded waggle dances to see if the advertised dances matched the found resources in the landscape. Two pollen samples were collected, waggle dances were recorded and decoded, and the landscape was mapped within a 3 km radius from the observation hive in Hinnerup, Denmark, over a course of two days in May 2018. The results of the experiment indicated that honey bees prefer the most abundant (and probably the most profitable) resources in the landscape, such as oilseed rape (*Brassica napus*) and fruit trees (*Prunus spp. / Pyrus spp*.). Mapping of the landscape corresponded to the found pollen species in pollen samples, and the decoded waggle dances showed a preference for the largest and densest oilseed rape fields. Interestingly, fruit trees were the most represented pollen species in the pollen samples, even though oilseed rape was more abundant in the landscape. Possible explanations for this are discussed in the report. This study proved that pollen samples, the waggle dance and mapping of the landscape can, in combination, be used as an indicator of where honey bees forage. In conclusion, the most important pollen sources for our honey bees were fruit trees and oilseed rape, which is in accordance with the expected abundant resources in spring in Denmark.

Resumé

Honningbier (*Apis mellifera*) falder i antal verden over. Da de er vigtige både økonomisk og økologisk, er det afgørende, at vi lærer mere omkring honningbiers velbefindende. I dette studie var formålet at undersøge, hvilke pollenkilder der er de vigtigste for honningbierne i foråret. Til dette formål benyttedes pollendata samt kortlægning af det omkringværende landskab ved observationsstadet. Begge dele blev sammenholdt med afkodede svansedanse for at se, om de reklamerede danse stemte overnes med de fundne ressourcer i landskabet. To pollenprøver blev indsamlet, svansedanse blev filmet og afkodet, og landskabet blev kortlagt indenfor en 3 km radius fra observationsstadet placeret i Hinnerup, Danmark, over en periode på to dage i maj 2018. Resultaterne af eksperimentet indikerede, at honningbierne foretrak de mest abundante (og sandsynligvis mest indbringende) ressourcer i landskabet, herunder raps (*Brassica napus*) og frugttræer (*Prunus spp. / Pyrus spp*.). Kortlægning af landskabet svarede til de fundne pollenarter i pollenprøverne, og de afkodede svansedanse viste præference for de største og mest tætbevoksede rapsmarker. Interessant nok var frugttræer de mest repræsenterede i pollenprøverne, til trods for at raps var den mest abundante ressource i landskabet. Mulige forklaringer på dette diskuteres i rapporten. Dette studie viste, at pollenprøver, svansedanse samt kortlægning af landskabet kan, når det sammenholdes, bruges som en indikator for, hvor honningbier fouragerer. Det kan konkluderes, at de vigtigste pollenkilder for vores honningbier var frugttræer og raps, hvilket stemmer fint overens med de forventede abundante ressourcer i det danske forår.

Introduction

The social honeybees (*Apis mellifera)* are just as interesting as they are important ecologically and economically. They are known to be generalists as a species, but very specialized (flower constant) on an individual level (Pankiw and Page Jr. 2000; Kyger et al. 2011). This makes them important quantitative pollinators and therefore one of the most important pollinators of many plants in Denmark (Hansen et al. 2006). Honey bees live in large families typically consisting of one queen, a smaller number of drones and many thousand worker bees (Seeley 1995). Every bee in the colony goes through four life stages: egg, larva, pupa and adult. It is the worker bees' job to clean up the hive, feed the larvae and the queen, produce honey, collect pollen, nectar and water, and so forth, depending on the age of the worker bee (Seeley 1995). Once the bees are fully developed, they spend the rest of their lives collecting resources for the colony (Seeley 1995).

Because honey bees live in these large colonies, they need an equivalently large amount of food, as well as a balanced diet; 120-200 kg nectar and an average of 26 kg pollen pr. year (Kryger et al. 2011). For this purpose, they have developed a unique method for communicating with the colony about good resources; the waggle dance. This dance consists of two faces; a so-called waggle run, where the bee vibrates its body from side to side while walking in an angle relative to the vertical comb, and a return phase, where the bee simply returns to the starting point (Grüter and Farina 2009). The duration of the waggle run determines the distance to the resource, and the angle compared to the vertical comb determines the direction relative to the sun (Grüter and Farina 2009). Zarchin et al. (2017) found that honey bees might dance faster for resources which the colony lacks, and Couvillon and Schürch found that honey bees are economic foragers, which means they only use time and energy following waggle dances that upweight the benefits compared to the costs (Couvillon et al. 2014). However, we still do not understand the complexity of the waggle dance completely, and many studies suggest this communication method is not necessarily an accurate way of determining where the honey bees collect their resources (Couvillon et al. 2012; Al Toufailia et al. 2013; Schürch et al. 2016). Studies have shown that there is intra-dance variation, inter-specific variation and miscalibrations to consider, which ultimately means foragers are spread over a patch in the landscape (Couvillon et al. 2012; Preece and Beekman 2014; Schürch et al. 2016). But, even though the waggle dance might not be 100% precise, it is suggested that the bees dance the best they can, as for their nestmates to have a chance of finding the good resources (Preece and Beekman 2014).

Even though the waggle dance is not accurate, it can be used to assess where the honey bees forage. Honey bees can fly up to ~10 km for food, but they mostly forage within a 2-3 km radius from their hive (Seeley 1995; Dupont and Søgaard 2017). Partly due to plowing, the number of flower-rich biotopes has decreased, which is one of the reasons why honey bees are declining in numbers (Strandberg and Krogh 2011). Especially during summer, honey bees have difficulties finding good pollen- and nectar sources due to the thrifty landscape, so they must fly farther away from the hive, and these resources are not necessarily of better quality (Couvillon et al. 2014). Naturally, the honey bees forage on different pollen- and nectar sources throughout the season due to the shifting flowering phenologies of different plant species (Christensen 2013). However, when honey bees have found a profitable resource, they tend to exploit it for as long as possible. They do this partly because it is costly for a forager bee to switch to a new source, and partly because they are good at passing on information about good pollen sources (Dupont and Søgaard 2017).

My part of the study has a focus on which pollen sources the bees collected pollen from, and whether it was possible to map the landscape sufficiently to match the collected pollen samples. The aim of this study was to use pollen data and maps to estimate where the honey bees collected their resources in an agricultural landscape in Denmark, and to assess whether the waggle dance is a reliable method to detect the pollen resources used by the colony. We expected oilseed rape (*Brassica napus*) and fruit trees (*Prunus spp. / Pyrus spp.*) to be abundant in the pollen samples, as these were expected to be the most profitable resources for honey bees in May (Christensen 2013). In continuation to this, I wanted to investigate which factors affect the food search of honey bees; what makes up a good resource? How does the change in season affect the resource collection? Which consequences are related to the decrease in flower-rich biotopes?

Materials and Methods

Observation hive and setup

We carried out the experiment in early spring in a town called Hinnerup, Denmark, where the most important resources for honey bees are oilseed rape and fruit trees (Axelsen et al. 2011). One colony of approximately 5000 honey bees (*Apis mellifera)* of the Buckfast variety was used. The colony was bought a few weeks prior to the beginning of the experiments to ensure it was not too big, and was placed on Emilsmindevej, Hinnerup (56.272307, 9.987220). The observation hive was custom made with a single windowpane and foam on the inside of the door to isolate it. The windowpane was connected to a super with room for 10 frames (*Figure 1*). The inside of the hive must sustain a core temperature around 34 degrees Celsius to ensure brood rearing (Seeley 1995). Therefore, it was crucial that we kept the observation hive warm when the door was open for filming, as to prevent unintentionally weakening the colony. To assure this, we used a small heater and placed it right in front of the windowpane, when the door was open. This also prevented condensation and therefore assured better video quality. We used a Sandstrøm Full HD 1080P webcam on a tripod to record the waggle dances. To make sure the webcam had a horizontal reference frame, which could be used to measure the angles of the waggle dances later correctly, we included the frame around the windowpane in our recordings. The camera was directly connected to a computer, where we used Windows Movie Maker (version 2012) for the recordings. For the accuracy of further analysis of the waggle dances, we ensured that the frames of the observation hive were placed perfectly horizontally on the ground using a bubble level. To make sure the honey bees did not get confused by direct sunlight, and to minimize reflection on the windowpane, we constructed a self-made tent around the whole setup (*Figure 1*). This, too, contributed to keeping the hive warm.

Figure 1. Photos by: Julie Ørnholm Frederiksen. Observation hive and setup.

Pollen collection and analysis

For collecting pollen, we used a manual method instead of a pollen trap, as there was not sufficient space for one such trap on the entrance to the observation hive. We caught the honey bees using a net, and we made sure to catch pollen-collecting bees throughout the period where we recorded waggle dances as well, as to get an estimate of pollen gathered throughout the day. Pollen pellets were removed from the bees using finger nail files (*Figure 2*). Removed pollen pellets were put in separate test tubes and marked separately for each collecting date. Pollen pellets were removed from the collected bees either by freezing (7th May 2018) or by cooling them down with cooling elements and releasing them afterwards (8th May 2018). A total of 22 bees were collected on 7th May and 38 bees on 8th May.

The two pollen samples (0.34 g and 0.67 g) were sent to QSI, a laboratory in Germany specialized in pollen identification. Each sample contained several thousands of pollen grains, of which the laboratory classified 500 random pollen grains to type, mostly to plant genus, and more rarely to species or family level (hereafter pollen species). They use a standard method, where the pollen samples are suspended in water and thoroughly mixed, after which they take a drop of the sample and count 500 pollen grains. For every pollen species the proportional representation in the pollen sample was assessed. The palynological analysis was conducted according to German DIN 10760:2002-05. Identification of pollen followed melissopalynological literature and databases (Beug 2004, https://www.paldat.org, http://ponetweb.ages.at). In the quantitative analysis, the pollen species was considered insignificant to the honey bees if there were only 1-2 pollen grains of the species in a sample (Dupont and Søgaard 2017).

Figure 2. Photos by: Annika Skardsa Jeppesen. We removed pollen pellets with nail files from the honey bees' legs after cooling them down on May 8. In the photo to the left is a bee lying on the mat to get warm.

Mapping of the landscape

To map the landscape surrounding the observation hive, we used the Danish website called Danmarks Miljøportal (https://arealinformation.miljoeportal.dk/html5/index.html?viewer=distribution). On an orthophoto from spring 2018, we marked all the relevant conservation areas, including meadows, heathlands, swamps, water meadows, marshes, lakes and natural fences, such as bushes and trees, which are the natural areas where honeybees most likely collect their food sources. In addition to the natural areas, we marked flowering crop fields (oilseed rape) and hedgerows. Once these areas were marked on the map, we went out and sketched all relevant food sources within a radius of 3 km from the observation hive onto that same map. To divide the food sources properly into relatively good and less good areas, we used a sheet subdivided into nine categories; both for herbs, bushes and trees (*Appendix 1*), dividing the resources based on density and size/area. Since honey bees prefer large food sources, we generally did not include pollen sources in the categories low density/small area, low density/medium area and medium density/small area, unless they were very close to the observation hive. The bees should, according to our knowledge, not include these areas in their diet. Every time we found a significant pollen source, we marked it on the map with a number and noted the density/area plus species on the sheet. For an overview over the resources found, see Table 1.

Once the waggle dances were decoded, we sent the UTM endpoints to a GIS specialist who plotted the endpoints onto a layer of the landscape around the observation hive. I then edited the map in Paint (version 1803), where I sketched all the found pollen resources in the area; oilseed rape (*Brassica napus*), wild cherries (*Prunus avium)*, dandelions (*Taraxacum officinale),* blackthorn (*Prunus spinosa)* and lady's smock (*Cardamime pratensis*) as well as added the UTM endpoints and the coordinates for the observation hive (*Figure 4*). This way, it was possible to match the UTM endpoints with the resources more easily.

Analyzing recordings of waggle dance

Three days prior to the experiment, we did a preliminary test of a semi-automatic method in which waggle dances were video recorded and decoded manually. Previous studies have either used a fully manual or a fully automatic method, but since a fully automatic method is expensive in equipment, and a fully manual method is very comprehensive (see report made by Annika S. Jeppesen for more information), we wanted to see if a mix of both was possible.

As described under "Observation hive and setup", we used a webcam to record the honey bees' waggle dance inside the hive. We made 10-minute recordings approximately twice every hour from 10:30 to 15:10, where the bees are most active, over two days in May with warm and calm weather. Recordings were made both for mornings and afternoons in order to see if diurnal variation was found for pollen resources collected by honey bees, or if they danced for the same resources throughout the day. Once we had enough recordings, my partner and I went home and divided the videos in two, so we both analyzed an equal amount. There was a total amount of 2 hours and 20 minutes (14 videos) of recordings, so we each analyzed 1 hour and 10 minutes (7 videos). We used approximately 30-45 minutes analyzing each video, a total amount of circa ~10 hours. In this report, I use all data when estimating whether the waggle dances are a reliable way of assessing the used resources.

Figure 3. Waggle dance angle measurement in Excel, with the arrow pointing in the direction of the dance.

To estimate where the bees collected pollen, our co-supervisor, Peter Borgen Sørensen, had developed a macro in Excel with the coordinates of the observation hive, year, month and date to calculate the azimuth. With this macro, it was possible to measure the angle as well as the time spent during the waggle run. We simply had to clip out a picture of a bee in one of the videos and copy paste it in the Excel file for angle measurement (*Figure 3*), along with noting the duration of the waggle run. As output, the macro made an estimate of the direction and distance flown, resulting in the UTM endpoints for which the bees supposedly danced. By comparing these endpoints with the mapping of the landscape, we could see whether the waggle dance is a satisfactory way of calculating where the bees found their pollen or not. It was crucial that we did these estimates as correctly as possible. Therefore, we only took the bees which were more or less consistent in both angle and time, and measured four rounds of the same bee's dance to get a mean value of the duration of the dance, as studies have shown that a mean of four waggle runs, not including the first and the last run, gives the most precise estimate (Couvillon et al. 2012). There were more dancing bees on the second day compared to the first; 97 and 130, respectively. However, we did not measure *all* the bees in the video recordings. Many of them were inconsistent in their dances, or they were simply covered by too many bees for us to assess the dance correctly, so we only decoded dances from bees that we thought would cause less bias. For further information about the method, see Annika S. Jeppesen's report.

Results

Mapping

We observed a total of 33 potential flower (and therefore pollen) resources in the landscape, divided into oilseed rape (*Brassica napus*), wild cherry (*Prunus avium*), common dandelion (*Taraxacum officinale*), blackthorn (*Prunus spinosa*) and lady's smock (*Cardamime pratensis*). As illustrated in table 1, the resources of greatest coverage were made up of oilseed rape, wild cherry and the common dandelion, with oilseed rape being the most abundant of them all, which is in accordance with the expected resources in May (Christensen 2013). We decided not to categorize the pollen resources in the smaller towns within the circle, because these were made up of various fruit trees, garden flowers and so forth, and it would be comprehensive to classify all of them when we were not allowed in the gardens. Therefore, we agreed that if the dance data should show significant interest in these towns, we would know that they were housing all sorts of different pollen species. Moreover, we noted that on the farm, in close vicinity to the observation hive, there were two giant maple trees (*Acer sp*.) and several fruit trees, including cherries (*Prunus spp*.) and apples/pears (*Pyrus spp*.). Furthermore, the neighboring farm had an orchard, and therefore numerous fruit trees.

Table 1: An overview over the abundant pollen sources within a 3 km radius from the observation hive. As seen in the table, it is obvious that the most important pollen sources in the landscape was oilseed rape (Brassica napus), wild cherries (Prunus avium) and dandelions (Taraxacum officinale). As we mapped the landscape over a course of two days, both 7th May and 8th May is represented in the table. We assume the flowering of the respective flower species is roughly the same for both days.

Date	Area number	Species	Area covered / size of plant	Coverage/ number
07-05-2018	10	*Brassica napus*	Large	High
07-05-2018	1	*Brassica napus*	Large	High
08-05-2018	28	*Brassica napus*	Medium	High
08-05-2018	25	*Brassica napus*	Small	High
08-05-2018	24	*Brassica napus*	Small	High
07-05-2018	9	*Brassica napus*	Large	Medium
07-05-2018	4	*Brassica napus*	Medium	Medium
08-05-2018	15	*Brassica napus*	Medium	Medium
08-05-2018	31	*Brassica napus*	Medium	Medium
08-05-2018	22	*Brassica napus*	Medium	Medium
07-05-2018	13	*Brassica napus*	Medium	Low
07-05-2018	2	*Prunus avium*	Large	Many

08-05-2018	26	*Prunus avium*	Large	Many
07-05-2018	8	*Prunus avium*	Large	Many
08-05-2018	27	*Prunus avium*	Medium	Many
07-05-2018	6	*Prunus avium*	Large	Some
08-05-2018	20	*Prunus avium*	Large	Some
07-05-2018	3	*Prunus avium*	Large	Some
08-05-2018	17	*Taraxacum officinale*	Large	High
07-05-2018	12	*Taraxacum officinale*	Medium	High
07-05-2018	6	*Taraxacum officinale*	Medium	High
07-05-2018	11	*Taraxacum officinale*	Small	High
08-05-2018	29	*Taraxacum officinale*	Small	High
07-05-2018	7	*Taraxacum officinale*	Large	Medium
08-05-2018	32	*Taraxacum officinale*	Large	Medium
08-05-2018	18	*Taraxacum officinale*	Large	Medium
08-05-2018	21	*Taraxacum officinale*	Medium	Medium
08-05-2018	14	*Taraxacum officinale*	Small	Medium
08-05-2018	30	*Taraxacum officinale*	Medium	Medium
08-05-2018	16	*Taraxacum officinale*	Small	Medium
08-05-2018	19	*Taraxacum officinale*	Medium	Low
07-05-2018	5	*Prunus spinosa*	Large	Some
08-05-2018	23	*Cardamine pratensis*	Small	High

Pollen samples

Pollen analysis showed that the pollen samples consisted of pollen from fruit trees (*Prunus spp. / Pyrus spp.)*, oilseed rape (*Brassica napus*), maple (*Acer sp.*) and dandelion (*Taraxacum sp.*), with fruit trees being the most highly represented species followed by oilseed rape and smaller amounts of maple and dandelions (*Table 2*). It appears that fruit trees were equally important both days, whereas the honey bees found oilseed rape less attractive on the second day compared to the first. This might be because the maple tree right next to the hive flourished more on 8th May compared to 7th May.

Table 2: Percentage of the identified pollen species; fruit trees (Pyrus spp. / Prunus spp.), oilseed rape (Brassica napus), maple (Acer sp.) and dandelions (Taraxacum sp.) on 7th May and 8th May.

Pollentype	07-05-18	08-05-18
Pyrus spp. / Prunus spp.	50	51
Brassica napus	46	34
Acer sp.	2	9
Taraxacum sp.	2	6

Waggle dance decoding

As illustrated in Figure 4, the honey bees predominantly danced for the oilseed rape fields in the northwestern part of the 3 km circle. These were the ones marked with highest densities (10 in figure 4). The oilseed rape fields to the northeast were the second most flowering oilseed rape (1 in figure 4), where the ones to the south were less flowering. When it comes to identifying which dandelions and wild cherries the honey bees danced for, it is less apparent because the UTM endpoints are more scattered in the areas where these were abundant, and the patches of wild cherries and dandelions are generally smaller compared to oilseed rape. This makes it challenging to determine if the honey bees were actually dancing for these areas, because the endpoints are so scattered around the patches, as an apparent consequence of the waggle dance uncertainties (described in Annika S. Jeppesens's report). The best patches (according to table 1) of wild cherries were to the north/north east (2 and 8 in figure 4) and south east (26 in figure 4), whereas the best dandelion fields were to the southwest (12 and 17 in figure 4) and to the north (6 in figure 4), although it is uncertain whether the bees danced for these.

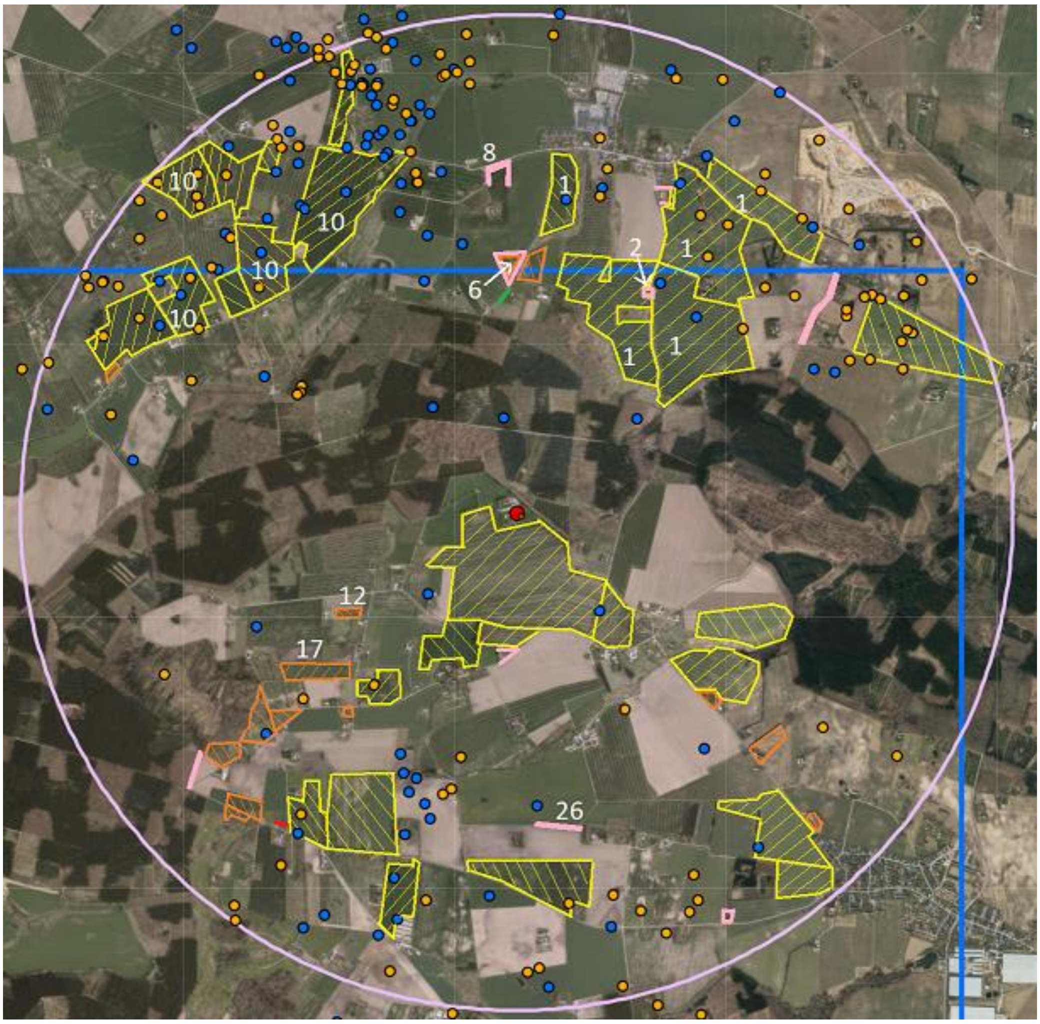

Figure 4: Map of the landscape surrounding the observation hive. Sketched areas are the significant pollen sources found within a 3 km circle from the observation hive. Yellow: oilseed rape. Orange: dandelions. Pink: wild cherries. Green: blackthorn. Red: lady's smock. UTM coordinates are marked with blue points for 7th May and orange points for 8th May. The red point in the middle are the coordinates for the observation hive (56.272307, 9.987220). Marked with numbers are the resources with the highest scores according to Table 1.

When we made diagrams over which UTMx and UTMy coordinates the honey bees danced for over the span of a day, it was clear that they did not dance for different sources in the morning compared to the afternoon (*Figure 5*). Had there been a difference, we would have seen more patches of data points in different UTMx and UTMy coordinates when looking at the morning vs afternoon recordings, but this is not the case. The honey bees seemed to be very consistent.

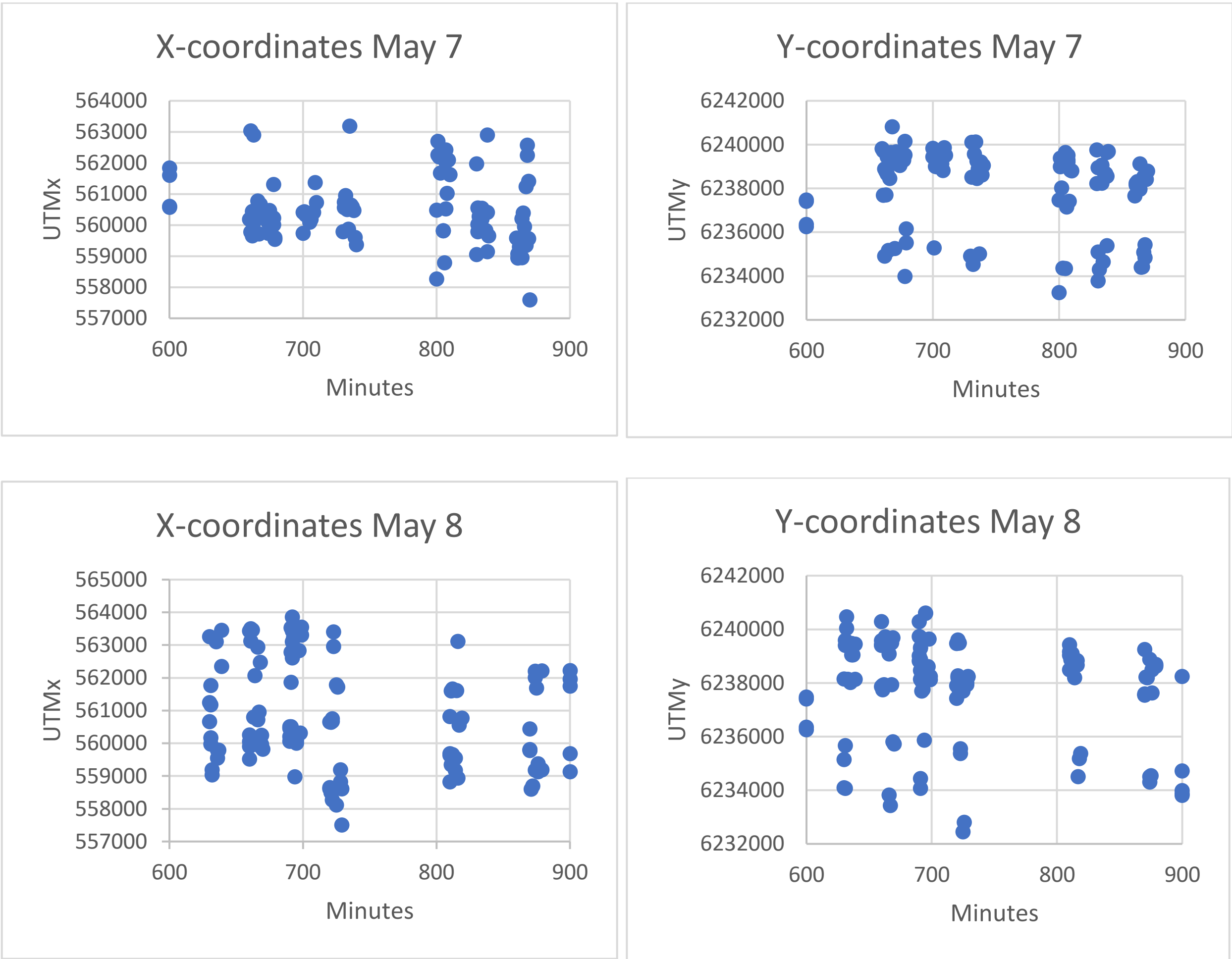

Figure 5. UTMx and UTMy coordinates for the two days of recording, divided into mornings (600-750 minutes) and afternoons (800-900 minutes). On the x axis is number of minutes after midnight, and on the y axis the x- and y-coordinates, respectively. It is apparent that the honey bees danced for the same resources during the whole day both days, as there seems to be no clear difference when looking at the diagrams.

Discussion

Honey bees' need for a balanced diet

In our study, we found oilseed rape and various pome and stone fruit trees to be the most used pollen sources, which corresponds to what we expected. However, that fruit trees posed a higher percentage (50% and 51%) in our pollen samples compared to oilseed rape (46% and 34%) is rather interesting, as oilseed rape is the most frequently used pollen source for honey bees on a national scale (Kryger et al. 2011). This leads to speculation in whether honey bees are able to distinguish between good and bad food sources. In this section, I will present the current knowledge on this field.

Honey bees, like every other living organism, need a balanced diet (Hendriksma and Shafir 2016; Zarchin et al. 2017). Pollen contains both protein, lipids, minerals and vitamins (Herbert 1992), which means it is a very important food source for honey bees. Different plants contain different amounts of pollen, and especially the total protein content and the composition of amino acids is known to differ among plant species (Roulston et al. 2000; Weiner et al. 2010). Previous studies have demonstrated that honey bees need 10 essential amino acids, which they are incapable of synthesizing themselves, hence they need to consume them through their diet (Degroot 1953). Generally speaking, the amount of amino acids in different pollen species are positively correlated to the proportion of protein in the respective pollen species. Most plants sustain all 10 crucial amino acids, but dandelions lack one (Keller et al. 2005a). This might be one of the reasons why dandelions are not as abundant in our honey bees' diet as is e.g. oilseed rape. Oilseed rape contains substantially more protein (30%) compared to that in dandelions (11%) (Christensen 2013). In comparison to these, cherry plums (*Prunus cerasifera*) contain 44% protein, and various other fruit trees contain high amounts of protein as well (Christensen 2013). If bees are able to differentiate between various pollen species, this indicates that they prioritize pollen with higher protein content.

But are honey bees, in fact, able to distinguish between good and bad foods? Some studies have shown that honey bees do have a preference when given the opportunity to choose between different pollen sources, but whether this is due to the nutritional components, or simply due to the different visual properties of different pollen species (Lunau 2000) is currently unknown (Keller et al. 2005a). Some studies have shown that honey bees take into consideration what the colony is lacking when they consider if a pollen source is good or not. This could imply that they prioritize nutrients that the colony needs (Simpson & Raubenheimer 2012; Hendriksma & Shafir 2016; Zarchin et al. 2017).

That our bees gathered more fruit tree pollen compared to oilseed rape pollen could indicate that honey bees are in fact able to distinguish between good and less good foods. Availability of high quality pollen and/or maple and fruit trees in the immediate vicinity of the observation hive could be another reason why oilseed rape is not the most collected pollen species, even though it was the most abundant resource at the time (*Figure 4*). It could of course be a combination of the two; since the fruit trees were easily available and they seem to have a higher nutritional value, it would make sense for the honey bees to concentrate their foraging on these.

Another explanation could be that different pollen species have different morphologies, thus some are bigger than others (Raven et al. 2005) and therefore the bees may not be able to carry as many pollen grains from flowers with larger pollen grains. If e.g. fruit tree pollen grains are smaller than oilseed rape pollen grains, it would make sense that the bees can carry more fruit tree pollen grains compared to oilseed rape. This would lead to the apparent assumption that our honey bees preferred fruit tree pollen over oilseed rape, when in reality it may be that the bees visited both oilseed rape and fruit trees equally often. However, according to our pollen analysis (*Table 2*), the oilseed rape pollen percentage dropped from 46% to 34% from one day to the other, whereas the fruit tree pollen percentage did not, suggesting that the bees did, in fact, prefer fruit tree pollen.

As illustrated, both amino acids and protein content seem to be essential for the honey bees, but because little is known about the bees' dietary needs, it is challenging to find appropriate ways of assessing what is most important for the bees. Although we do know that pollen is more important during brood rearing due to the larvae's consumption of protein rich food jelly, and nectar is more important when producing honey for overwintering (Seeley 1995; Couvillon et al. 2015), we do not know to which extent protein and amino acids are needed. It is therefore difficult to say whether the preference for fruit tree pollen in our samples was due to nutritional preference, visual differences, morphology of different pollen species or something else.

Pollen requirement

We observed that fewer bees came back with pollen on the first day compared to the second. It was warm and there was practically no wind both days, so the differences in pollen collection rate could not be caused by the weather, as Visscher and Seeley demonstrated could be a factor in their study of honey bees' foraging strategy (Visscher and Seeley 1982). The demand for pollen stays roughly the same through the entire season (May-September), although the pollen availability fluctuates (Seeley 1995). Because of the shift in pollen availability, honey bees create a stock of pollen within the hive for scarcer periods, to ensure the sustainable availability of proteins and nutrients for the brood and the worker bees (Seeley 1995).

Pollen is used and consumed by both developing worker bees and larvae (Keller et al. 2005b). Some forager bees are specialized in collecting pollen, others nectar, which results in the honey bee family as a working unit collecting resources from many different flowers at the same time (Kyger et al. 2011). A honey bee colony needs somewhere between 17-34 kg of pollen pr. year, depending on the size of the colony (Keller et al. 2005a). The bees strive to have approximately one kg of pollen stored in the hive at all times, which is sufficient for circa one week of bad weather or scarce flower sources (Seeley 1995).

The mechanism by which the bees know how much pollen they should collect is still being discussed. Some argue that the pollen forager bees consider the total amount of stored pollen in the hive when considering how important it is to collect more pollen (Fewell and Winston 1992). Another theory suggests that the pollen storage as such does not have any influence on the activity of pollen forager bees, but they rather react to the current need for pollen in the hive due to brood size (Hellmich and Rothenbuhler 1986; Fewell and Winston 1992). The bigger the brood, the more pollen is needed to feed them.

Whether the honey bees recruited more pollen forager bees on the second day due to scarcity of pollen in the hive, more brood to feed or something else, like the need for water was bigger on the first day and hence less bees came back with pollen, we cannot determine, because we did not look at the total pollen storage within the hive, nor did we keep track of the brood size. However, we noted that it had been a very hot weekend prior to the field days (Monday and Tuesday), thus it is plausible that the honey bees needed more water that Monday.

Is the waggle dance a reliable way of determining pollen sources?

Honey bees in our study showed a preference for the larger, more abundant pollen sources like oilseed rape and fruit trees, such as expected (*Table 2*). But is this reflected in the waggle dance data?

The oilseed rape to the northwest (10 in figure 4) of the observation hive was by far the most intensively flowering fields, and the decoding of waggle dances showed that the honey bees did indeed dance most frequently for these at the time of the recordings (*Figure 4).* It would make sense for the bees to dance substantially for these, because previous studies have shown that honey bees prefer abundant pollen sources, even though these do not give the best qualitative yield (Axelsen et al. 2011). On the other hand, we might have deselected, either unconsciously or due to difficulty seeing the bees, too many bees dancing for another food source, thus making the estimate of where the bees dance for biased. Also, honey bees do not only dance for pollen sources, but for nectar, water and resin as well, so the recorded dances may not all be for pollen, and there is of yet no way to distinguish between a dance for pollen and one for nectar or water (Couvillon et al. 2014), unless you collect the forager bee and determine what is in the crop. Therefore, some of the dances might have been for something else besides pollen. Furthermore, although we tried not to analyze the same dancing bee twice, it was difficult to keep track of the individual bees inside the observation hive. Hence, it cannot be ruled out that some of the data points are really the same bee analyzed twice. This should, however, not influence the statistical analysis.

Furthermore, some difficulties were associated with capturing the honey bees manually. When the bees came back from a foraging trip, they flew directly towards the entrance. Most of the time they were too quick for us to capture them with the net, hence it is random which bees we have caught. This is both an advantage and a disadvantage; an advantage because this makes sure the bees are not selectively caught, which ensures a random sample. On the other hand, it is a disadvantage because we cannot be sure whether the bees we have caught are a representative sample of the whole pollen collection from that day. However, the pollen samples from the two observation days match, which indicates that pollen samples were unbiased.

When looking at table 2, it is evident that the most used pollen source was various fruit trees, but it is difficult to determine whether some of the decoded waggle dances are in fact for some of the sketched fruit tree patches in figure 4. In areas with e.g. wild cherry, there are oilseed rape fields surrounding them. If the honey bees were dancing for these specific wild cherry patches, we would have expected to see a more clustered set of endpoints in these areas - if the waggle dance was to be a reliable way of determining resources in the landscape, that is. We did, however, observe a few round dances, where the honey bee simply dances around itself, because the food source is very close to the hive (Gardner et al. 2008). This would correspond to the maple and fruit trees located directly on the farm and the neighboring farm as well. Therefore, it might be that the decoded dances are not for fruit trees at all, but merely for oilseed rape (and dandelions), as the honey bees simply collected all their fruit tree pollen from the trees closest to the observation hive. Another explanation could be that some of the endpoints could be pointing towards the smaller towns where fruit trees were numerous, e.g. the patch of orange endpoints between the two oilseed rape fields to the southeast (*Figure 4*). Since we did not note which pollen sources were in town areas, we cannot be sure which fruit trees were in which town. However, we do know that almost all the small towns in the area had wild cherries (*Prunus avium*), sour cherries (*Prunus cerasus*) and several pome fruit trees (*Pyrus spp.*). Therefore, it seems likely that the honey bees might have danced for fruit trees in this particular town on 8th May. It could also be that the explanation is a combination of the two above; that the honey bees collected fruit tree pollen both from the farm and the neighboring farm, and from the small town to the southeast.

We experienced some difficulties mapping the landscape. We collected pollen, recorded waggle dances and mapped the landscape over the course of the same two days as to make a better estimate of the possible resources for the honey bees. We mapped half of the 3 km circle on 7th May and the other half on 8th May. We learned that the different oilseed rape fields were at different stages of flowering, thus making it challenging to determine whether they were of high or medium density (*Appendix 1*). On the second day, we came across the oilseed rape fields to the northwest, which proved to be the most intensively flowering fields of them all, but we had already marked some fields with high density on the first day. This forced us to realize that it is problematic to map the available resources in the landscape correctly, as you learn along the way how to differentiate the categories. Finally, because the pollen samples contained a fair amount of maple (*Table 2*), it might be that we have overlooked some flourishing maple trees in the landscape. These have light green flowers which are troublesome to differentiate from leaves when seen from a distance, making it plausible that we missed these. This means there might be some maple tree patches in the landscape which the honey bees danced for, but we cannot see it on the decoded waggle dances.

Finally, it is worth mentioning that the waggle dance is not perfect; there are uncertainties connected with using this method to distinguish where honey bees forage. We know from literature that honey bees can miscalibrate by as much as 50% (Schürch et al. 2016) and that there is intra-dance variation as well (Couvillon et al. 2012). This means that the same bee is not consistent in the way it dances, however it should not affect the analysis if our measurements are not 100% precise. For further information about the uncertainties connected with the waggle dance, see Annika S. Jeppesen's report. That said, it seems that the waggle dance is a good indication for where our honey bees found their resources in the landscape, especially when looking at the abundant oilseed rape fields.

Diurnal variation in waggle dances

Diurnal variation (morning versus afternoon) has been reported (Christian Petersen in Axelsen et al. 2011). In contrast to the results in our study, the bees had a tendency of collecting the same resources throughout the day (*Figure 5*). In these diagrams, it is clear that the honey bees more or less danced for the same resources all day, so for them to suddenly shift to new pollen sources later in the afternoon seems unlikely. Also, there was little variation in the landscape at the time of recordings; there were mainly considerable amounts of oilseed rape and some patches of wild cherries and dandelions, in addition to flowers in gardens of some small towns in the area. Hence, the honey bees may simply not have had any good alternatives and therefore were forced to dance for the same resources all day.

We recorded waggle dances from 11:00-14:35 on 7th May and from 10:30 to 15:10 on 8th May, so there is little variation in the time span. We do not, however, have recordings from the late afternoon/evening, so we do not know for how long the honey bees kept dancing, and whether they found new pollen sources later those days. Studies show that honey bees are quite consistent in their collection of resources, partly because they are good at passing on information about the good resources, and partly because it is costly for the bees to switch pollen source (Dupont and Søgaard 2017), presumably due to the increased search time associated with looking for new resources. Hence, we tentatively assume that even though we did not video record the bees later in the afternoon, it is likely that they simply continued to dance for the same resources as the ones we found when decoding the waggle dances.

The seasonal shifts in flowering

Different plants flower at different times during the season. As a consequence, honey bees are adapted for continuously searching the landscape for available food sources in order to take full advantage of the resource rich flowers when present. Studies show that honey bees are indeed good at localizing newly flowering resources, however the chance that they discover the new food sources decrease with distance from the hive (Seeley 1987). This makes sense because the farther the honey bees fly from the hive, the larger the area they must monitor. However, how do the seasonal shifts in flowering affect the food search for honey bees?

In early spring, honey bees need new supplies of both nectar and pollen, as they have used up their honey and pollen resources during winter. The production of brood begins in late winter, prior to the bees leaving the hive in early spring, hence it is crucial that foraging begins as soon as the weather allows the bees to fly, so the brood gets enough nutrition (Seeley 1995). In early spring there are plenty of both good nectar and pollen sources, such as oilseed rape, stone fruit trees and dandelions (Christensen 2013). The most important source during spring in Denmark is oilseed rape, in particular. This is because oilseed rape fields have a high coverage in agricultural areas in Denmark, hence the bees can get a quantitatively large yield out of using it (Axelsen et al. 2011; Kryger et al. 2011). Interestingly, oilseed rape does not contain as much nectar as e.g. fruit trees, but because oilseed rape is such an abundant food source, it is easier to find in the landscape, and distance to the resource has proven to be just as important as the yield, as they do not fly farther than need be (Seeley 1995). In our study, both fruit trees and oilseed rape were abundant in the pollen samples (*Table 2*). According to the waggle dance data, our honey bees collected most of their oilseed rape pollen from the northwestern fields, presumably because these were the densest (and therefore most profitable). Likewise, it is likely that the bees collected their fruit tree pollen from the trees on the experimental farm and the neighboring farm approximately 400 meters away, which means they did not have to fly very far. Thus, the bees chose to fly farther for a better oilseed rape source, whereas they did not have to fly far away to get fruit tree pollen.

The high abundance of flowers in spring contrasts to the scarcity during summer. Studies have shown that honey bees fly much farther from the hive during summer compared to both spring and fall (Couvillon et al. 2014), presumably because of the lack of good resources closer by. Especially between the flowering of oilseed rape in May and clover in June, there are almost no flowers present, which means the honey bees have to live off of their honey supply as to prevent starvation (Axelsen et al. 2011). For this reason, garden flowers have become important food sources for honey bees. Gardens may contain vital food sources when others are limited, as these might be some of the only patches with pollen during summer (Dupont and Søgaard 2017). During fall, there are almost no flowers for the honey bees, unless there is heather which flowers in August (Axelsen et al. 2011) or fodder radish (*Raphanus sativus var. oleiformis*) and yellow mustard (*Sinapis alba*) which flourishes in September/October (Christensen 2013).

There is substantial evidence that when food is scarce, honey bees tend to lower their standards, as they would otherwise get no food at all. On the other hand, when there is plenty of food sources, they increase the threshold for which flowers they find satisfactory, which ultimately means that only the best resources are danced for and collected (Stephens and Krebs 1986). This corresponds to our results, where it seems the bees would rather fly farther away from the hive to get to the better oilseed rape fields. Furthermore, Thomas Seeley found that on days with bad weather less honey bees go on foraging trips, and those that do generally stay close to the hive (Visscher and Seeley 1982). Studies have shown that honey bees can switch the main pollen resource from one year to the next, even though the distribution of the different pollen resources have not changed (Moezel et al. 1987). This might be because honey bees scout the area for the best resources, and once they have found a good one they stick with this source because it is costly for them to try and find a new one (Dupont and Søgaard 2017). Furthermore, the weather plays an important role as well, as the flowering periods vary with the climate.

Decrease in flower-rich biotopes

It has become an increasing problem that flower-rich biotopes are generally decreasing (Christensen 2013). These small biotopes are crucial for various bee species in Denmark during periods with a lack of flowering fields in the landscape (Christensen 2013). One of the major reasons why this is happening is weed control on cultivated land (Axelsen 2011). Holzschuah et al. (2007) found that organic wheat fields in Germany had a higher coverage of flowering plants, as well as a higher bee- and flower diversity compared to non-organic wheat fields. Other studies have found that organic fields contain more insect pollinated plants than plants which are not pollinated by insects (Gabriel and Tscharnkte 2007). The latter study also showed that there are generally more insect pollinated plants along the edge of the cultivated fields compared to the field center. These studies indicate that organic fields enhance plant and insect pollinator diversity, even though organic fields only represent 7% of the total amount of cultivated land in Denmark (Danish Agriculte and Food Council 2016).

In Britain, Carvell et al. (2006) investigated the decrease in important weeds for bumblebees in the twentieth century. Bumblebees and honey bees use many of the same resources (Theuerkauf et al. 2018), hence the results from this study can be put in perspective to honey bees. The study showed that many weeds, such as *Trifolium pratense* which is important for both species, is declining drastically presumably due to cultivation of the landscape and use of pesticides. Likewise, in Denmark, many roadsides were covered with clover, dandelions etc. in the 1960s, but today most of these roadsides are inhabited by various grasses (Christensen 2013). In Denmark, the cultivated land is very homogenized, and we sow still bigger amounts of corn each year, which is of poor nutritional value to honey bees (Axelsen et al. 2011). It is clear that the decrease in flower-rich habitats are not due to only one parameter affecting the areas, but several anthropogenic issues. Honey bees in Denmark, and many other European countries, are now predominantly domestic animals even though they used to be wild (Kryger et al. 2011). Partly due to the decrease in profitable flower resources and the invasion of the Asian varroa mite, which kills the bees without treatment, we see very few wild colonies in Denmark today (Kryger et al. 2011). In other words, if we want the bees to stay, we should consider getting more “bee-friendly”. This includes being more considerate when plowing fields, as to not accidentally destroy the flower-rich biotopes, planting more good flower resources for bees in parks, schools and gardens, avoid using pesticides and fertilizer on the roadsides, and so forth (Christensen 2013; Theuerkauf et al. 2018).

Conclusion

Honey bees in our study showed a clear preference for fruit trees (*Prunus spp. / Pyrus spp.*) and oilseed rape (*Brassica napus*) according to pollen samples, which is in correspondence to the season. Surprisingly, fruit trees represented the largest share of the collected pollen, even though they were less abundant compared to oilseed rape. However, it can be explained by the higher quality pollen and quantity of nectar in fruit trees as well as the fact that these were in close vicinity the observation hive.

It proved difficult to map the landscape properly; we could not spend too much time trying to write down all the pollen sources within the small towns, and we may well have overlooked some other sources. The seasonal shifts in flowering requires that honey bees are efficient in searching the landscape, in order to be able to exploit the resources whenever they are present. This study proves that honey bees are, indeed, good at this, or else they would not have found the better oilseed rape fields to the northwest.

Regarding the usefulness of the waggle dance to correctly assess where the honey bees collected their pollen, we can conclude that the decoded waggle dances did, in fact, point towards the most abundant oilseed rape fields in the landscape. This corresponds to the contemporary assumption that honey bees upweight costs and benefits when dancing for resources. Together with the landscape analysis, we were able to make an educated guess to where the honey bees found their pollen sources, but it was not 100% precise. Furthermore, data showed that our bees danced for the same resources throughout the day.

If honey bees are to continue being able to survive in the Denmark, it is important that we think about which flower sources are available in the landscape, as most of the flower-rich biotopes are slowly decreasing in numbers. Honey bees need a balanced diet, so for them to thrive we need to think in more bee-friendly manners, like sowing more diverse plants and being careful when plowing the fields.

Acknowledgements

First, I would like to thank Annika Skardsa Jeppesen for choosing me as her partner for this project. You and I have proven to be a great team, and I am so grateful for your friendship and partnership.

A special thanks to my main supervisor, senior scientist Yoko Luise Dupont, for her continuous good advice and ability to keep us focused and delighted that we chose her as our counselor. You have been of great help, and I look forward to working together with you some time in the future.

Senior scientist Peter Borgen Sørensen, my co-supervisor, also deserves some huge thanks for technical help and the many laughs over our insufficient know-how in Excel. It is safe to say that I have learned equally as much in Excel as I have learned about honey bees during this project.

A huge thanks to Vibeke and Knud Simonsen for borrowing us your lovely farm, and for always being so kind. Had you not allowed us in your home, there would have been no reports and no bachelor's degree for us.

Finally, I would like to thank Harry Andreassen for building our very own combined observation hive. It was just perfect for this pilot study, and we were very impressed, to say the least.

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Appendix 1: Sheet over how we divided the different categories of flowers in the landscape. For each resource, we gave it a number, estimated how big the area/size was and the abundance of the resource as well as noted the species.

Bedrift_Vibeke_Simonsen Area no: Date:

Weeds		**Density**		
		High	Medium	Low
Area	Big			
	Medium			
	Small			
Bushes		**Number os bushes**		
		Many	Some	A few
Size	Big			
	Medium			
	Small			
Trees		**Number of trees**		
		Many	Some	A few
Size	Big			
	Medium			
	Small			